Biogeography in Northwestern Africa: Distributions and ecological niches of *Gerbillus* rodents

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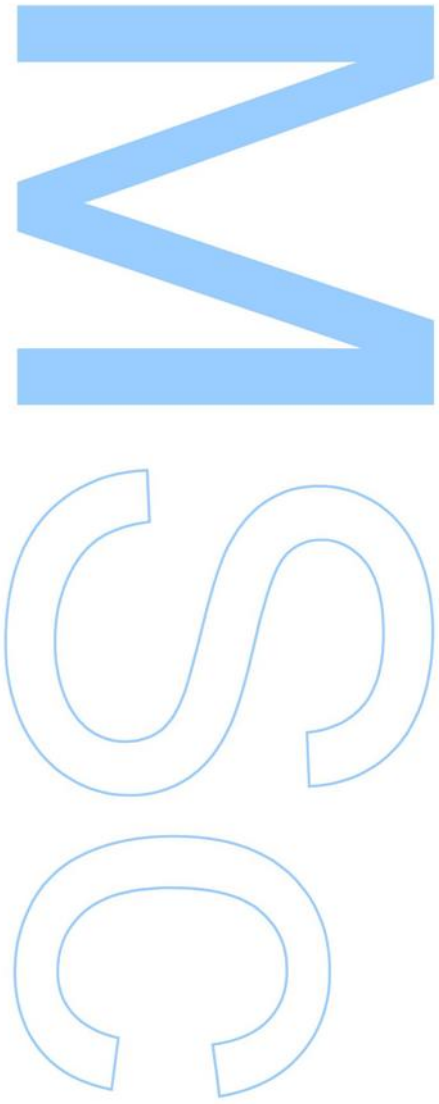

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Resumo

O Norte de Africa é uma região árida muito extensa, sendo muitas vezes esquecido por estudos biogeográficos devido a problemas sociopolíticos e de acessibilidade que dificultam o trabalho de campo. No entanto, a região é muito relevante para estudar padrões de biogeografia, tendo sido moldada por alterações climáticas dramáticas e contendo organismos adaptados a ambientes muito extremos. Particularmente, a costa ocidental do norte da África parece ser muito interessante para estudar biogeografia, devido à influência do Oceano Atlântico, topografia complexa e história de alterações do nível do mar. Nesta região, e seguindo uma tendência de identificação molecular cada vez mais acessível das espécies, algumas espécies de roedores de gênero *Gerbillus* foram encontradas em vários novos locais, para além de terem tido uma reordenação taxonómica. As distribuições de *Gerbillus* no Norte de África parecem sobrepor-se mais do que se pensava, levantando questões sobre como e onde as espécies coexistem e porque é que algumas áreas possuem uma maior riqueza de espécies do género do que outras. O objetivo principal deste estudo foi prever áreas adequadas para cada espécie e possíveis áreas de coexistência, bem como compreender as principais limitações climáticas e de habitat que moldam as distribuições.

Esta tese reúne dados de observação de 12 espécies de *Gerbilllus* em todo o norte de África, a maioria com confirmação molecular da identificação da espécie através de barcoding. Essas espécies (*G. amoenus, G. campestris, G. gerbillus, G. henleyi, G. hesperinus, G. hoogstraali, G. nancillus, G. nigeriae, G. occiduus, G. pyramidum, Gerbillus sp., G. tarabuli*) são aqui sujeitas a um estudo comparativo dos seus principais indicadores climáticos e de habitat através de Sistemas de Informação Geográfica (SIG) e Modelação baseada em Nichos Ecológicos (ENM). As reações das espécies aos constrangimentos climáticos foram usadas para projetar as suas distribuições para os climas passados do Holoceno Médio, Último Máximo Glaciar e Último Interglaciar, esperando mudanças de distribuição quando os níveis de precipitação eram maiores do que atualmente na área de estudo. Foram previstas áreas climáticas estáveis para cada espécie sobrepondo as suas projeções de distribuição dos diferentes períodos. De forma semelhante, a riqueza potencial de espécies foi prevista com a sobreposição dos modelos de nicho de todas as espécies. Os nichos topográficos e de habitat das espécies foram comparados com testes de overlap de nicho e de hipóteses, procurando qualquer conexão entre o overlap de nicho e relações filogenéticas, além de testar se os nichos são conservados entre espécies.

Os resultados deste trabalho mostram áreas adequadas para cada espécie no Norte de Africa, que juntamente com novos locais para observações de espécies fornecem uma sugestão de atualização das suas distribuições. A análise dos factores climáticos das espécies revelou que as variáveis de temperatura são, em geral, as mais importantes a condicionar distribuições, especialmente grandes amplitudes térmicas diurnas e anuais assim como temperaturas mínimas, uma vez que os animais são noturnos. A precipitação desempenhou um papel importante ao diferenciar algumas espécies, já que alguns *Gerbillus* evitam áreas com maiores níveis de precipitação, enquanto outras evitam áreas com níveis de precipitação quase nulos. Em algum nível intermédio (níveis de precipitação intermédio) poderá estar a maior riqueza potencial de espécies de *Gerbillus*, coincidindo com a hipótese da produtividade primária intermédia. As projeções para o passado revelaram mudanças insignificantes na distribuição das áreas adequadas no Holoceno Médio (húmido), uma vez que os intervalos de temperatura nesse período eram semelhantes aos do presente. As distribuições das áreas adequadas foram geralmente menores no Último Máximo Glaciar e mudaram substancialmente no Último Interglaciar, um período com amplitudes térmicas menores que deverá ter beneficiado todas as espécies. Quando se trata de eixos climáticos, topo-climáticos e de habitats, embora a sobreposição de nicho entre espécies tenha correspondido mais à sobreposição geográfica (sugerindo adaptação às condições locais), os nichos das espécies parecem estar relativamente conservados. Este conservadorismo relativo de nicho sugere alopatria como o principal mecanismo de especiação do género na região estudada. As espécies parecem assim selecionar variáveis ambientais semelhantes, mas estão restringidas por diferentes ambientes disponíveis onde eles existem.

Palavras-chave: Biogeografia, África do Norte, deserto, *Gerbillus*, roedores, mamíferos, nicho ecológico, ENM, SIG, Alopatria, Holoceno Médio, Último Máximo Glaciar, Último Interglaciar.

Abstract

North Africa is a very wide arid region, often forgotten in biogeography studies due to low accessibility and socio-political problems that hinder fieldwork. However, that region is very relevant to study biogeography patterns, having been shaped by dramatic climatic shifts and containing organisms adapted to very extreme environments. Particularly, the western coast of North Africa seems to be very interesting to study biogeography, due to the influence from the Atlantic Ocean, complex topography and history of changing sea level. In this region, and following the trend of increasingly affordable molecular identification of species, new data is accumulating for several species of *Gerbillus* rodents. *Gerbillus* distributions in North Africa appear to overlap more than previously thought, which raises questions of how and where species coexist, and why some areas have a higher species richness than others. It was the main aim of this study to predict suitable areas for *Gerbillus* species and possible areas of coexistence, as well as to understand the topo-climatic and habitat drivers shaping their distributions.

This thesis combines distribution data for 12 *Gerbilllus* species spanning over North Africa, most of it with molecular confirmation of species' identification through barcoding. These species (*G. amoenus*, *G. campestris, G. gerbillus, G. henleyi, G. hesperinus, G. hoogstraali, G. nancillus, G. nigeriae, G. occiduus, G. pyramidum, Gerbillus sp., G. tarabuli*) are here subject to a comparative study of their topo-climatic and habitat drivers by using Geographical Information Systems (GIS) and Ecological Niche-based Modeling (ENM). The species reactions to climatic drivers were used to project their distribution to the past climates of Middle Holocene, Last Glacial Maximum and Last Interglacial. Stable climatic areas were accessed for each species by overlapping their distribution projections of different periods. In a similar way, potential species richness was accessed by overlapping the niche models of all species. The topo-climatic and habitat niches of the species were compared with niche overlap, identity and background tests, striving to find any connection between niche overlap and phylogenetic relatedness, asking if the niches are conserved between species.

The results of this work show suitable areas for each species in North Africa, which together with novel geographical locations provide an update for species distributions. The analysis of climatic drivers revealed that temperature variables are generally the most important predictors of distributions. Especially large diurnal and annual temperature ranges as well as low minimum temperatures on the coldest month constrain niches. Precipitation played a role differentiating species, as some *Gerbillus* avoid areas with relatively high precipitation levels while others avoid areas with almost

null precipitation levels. Somewhere in between (intermediate precipitation levels) appears to be the highest potential species richness of *Gerbillus*. Projections to the humid Middle Holocene revealed insignificant suitability distribution changes, as temperature ranges in this period were similar to current day. Suitability distributions were generally smaller in the colder Last Glacial Maximum and changed substantially in the Last Interglacial, a period with smaller temperature ranges that should have benefited all species. When concerning climatic, topo-climatic and habitat variables, niche overlap between species was observed to correspond to geographical overlap suggesting adaptation to local conditions. However, the niches of the species appear to be relatively similar, suggesting niche conservatism. Relatively high niche conservatism predicts allopatry as the main speciation engine of the genus in the studied region. The species appear thus to select similar environmental variables, even when different geographic distributions expose them to different available environmental variation.

Keywords: Biogeography, North Africa, desert, *Gerbillus*, rodents, mammals, Ecological niche, ENM, GIS, Allopatry, Middle Holocene, Last Glacial Maximum, Last Interglacial.

Index

Table index

Figure Index

Glossary

AUC – Area under the receiver operating characteristic (ROC) curve, known as the AUC, is used as a measure of the overall fit of the models (Liu et al., 2005).

Fundamental niche – The full range of conditions (biotic and abiotic) and resources in which a species could survive and reproduce, without considering the interference of inter-specific competition and barriers to dispersal (Soberon & Peterson 2005; Sillero 2011).

Continuum hypothesis – Hypothesis that considers both aspects of ecological niches and stochasticity to explain distributions of species (Gravel et al. 2006).

ENM – Ecological Niche Model.

GIS – Geographical Information Systems.

GPS – Global Positioning System.

Operative temperature – Temperature that is experienced by animals, rather than the air temperature. It is affected by wind, humidity, exposure to the sun, contact with soil, sheltering (Bakken 1992).

Realized niche – The part of the fundamental niche that an organism occupies in reality as a result of limiting factors as inter-specific competition (Sillero 2011).

ROC curve – Receiver operating characteristic curve. It is the function of sensitivity (probability of true detection) versus probability of false detection of models, under varying thresholds (Lobo et al. 2008)

Unified Neutral Theory of Biodiversity and Evolution – Theory that discards basic ecological principles like niches in favor of stochastic Hardy-Weinberg population dynamics to explain evolution and distributions.

Vicariance – The process of loss of connectivity between populations of a species, either due to geographic or ecological barriers.

1 Introduction

1.1 Background

1.1.1 Biogeography

Studies and conservation decisions regarding biodiversity should be based on the most profound understanding of species distributions. Knowing exactly where the species exist both in the present and past is useful for example to plan studies of genetic diversity (Hewitt 2004; Brouat et al. 2007) and decide species conservation status (Vale et al. 2012), as well as to design conservation areas representative for biodiversity (Kati et al. 2004; Brito et al. 2016). It is the aim of biogeography to provide a comprehensive understanding on the distributions of species, in context with current and historical barriers to dispersal, and striving to find causality relationships between the distributions and the species reaction to biotic and abiotic factors (Crisci et al. 2003). Whenever environmental factors that are relevant for a species change in time, there are three possible outcomes for its populations: adaptation, migration or extinction (Aitken et al. 2008), which often leads to fragmentation of distributions. The process of connectivity loss between populations, coined “vicariance”, can have an influence in the genetic pool of populations (Bryja et al. 2014), promoting allopatric lineage divergence and eventually speciation (Kozak & Wiens 2006). Vicariance has been extensively studied when caused by physical barriers, like water bodies for terrestrial species (Zink et al. 2000), but less when the causes are purely ecological, as for example increased aridity (Mairal et al. 2017).

The recent developments in computational methods and remote sensing technology have brought the power to unravel complex distribution patterns, as well as corresponding underlying constraints. The combination of Ecological Niche-based Modelling (ENM) and Geographical Information Systems (GIS) (Guisan & Zimmermann 2000) is used to predict species distributions, based on overlapping georeferenced observations with environmental variables (Haslett 1990). The models point out other areas with similar variables that could be inhabitable by the studied species (Brito et al. 2009) and can be especially relevant in large and remote study areas (Travaini et al. 2007). Additionally, by projecting models to different climatic conditions it is possible to answer complex questions, as e.g.: what were the refugia of biodiversity throughout past climatic changes (Keppel et al. 2012; Martínez-Freiría et al. 2015) or how the expected climate change is going to affect species distributions (Rebelo et al. 2010; Martínez-

Freiría et al. 2013, 2016). These inferences are only valid when considering that the distributional drivers of species are stable through time and that evolution doesn't change significantly the species, which has limitations (Martínez-Meyer et al. 2004). All this knowledge can be of high importance in the future for national and international authorities/conservation associations. As the natural environments of the planet are deeply altered, the survival of some wild species is under threat (Root et al. 2003). The consensus is that specialist species are the most vulnerable to environmental changes, spiraling to extinction and being often replaced by generalist species that are able to cope with unstable environments or thrive in humanized habitats (Clavel et al. 2011). It is therefore important to study the existing biogeography and biodiversity patterns before they become obscure or even disappear.

1.1.2 Ecological niche overlap, niche conservatism and niche differentiation

One of the central premises of ecology is that every species has own biotic and abiotic requirements and constraints, in what is defined has its ecological niche (Strøm 1946; Hutchinson 1957). As a consequence, species should have distinct responses to topo-climatic and habitat factors, which affects their geographic distribution (Peterson 2001; Keith 2009). Even though the variables regularly used in biogeography studies are quite simplistic and do not summarize the whole niche and constraints of the species, they can provide a representative approximation when using modern methods (Godsoe 2010). For example, precipitation does not affect many animals in a significant way, however it is often directly related with primary productivity, which is relevant for those same animals (Huber et al. 2011; Brown 1973). Following this idea, biogeography works with several terms to describe a species niche. The fundamental niche englobes the space and full range of conditions and resources in which a species could survive and reproduce when disregarding interferences of other species (Hutchinson 1957). The realized niche represents only the space and range of variables that a species really occupies in face of other limiting factors, e.g. biotic competition, dispersal barriers (Soberon & Peterson 2005; Sillero 2011). There are methods for dealing with both niche inferences, but it remains practical to work with the realized niche, since it is easier to infer and it should be more approximate to describe real species distributions (Holt 2003; Sillero 2011).

Inferring the responses of species to environmental variables opens doors to the discussion of many issues, including the degree of niche overlap between taxa (Turelli

1978), species coexistence and sympatry (Chesson 2000; Martínez-Freiría et al. 2008) and even potential for invasions, invasiveness, in other regions (Peterson 2003). The degree of niche-overlap is a particular interesting concept, since inter-specific relationships, like competition, might exist between species of similar niches (Hardin et al. 1960; Pianka 1974). Interesting evolutionary questions emerge from comparing niche overlap, geographic overlap and phylogenetic distances of species (Graham et al. 2004). How are these three factors related? Do sister species have similar geographical distributions? Or are they different? There is an ongoing discussion about the niche overlap of closely related species and how speciation occurs. On one hand, the niche overlap of species can correspond more to geographical overlap, being the result of convergent adaptation to similar environmental conditions (Warren et al. 2008). On the other hand, niches can be evolutionary conserved, meaning that the niche overlap corresponds to phylogenetic relatedness between species, or phylogenetic inertia (Peterson et al. 1999). In fact, niche conservatism has been put forward as an important mechanism promoting vicariance and posterior speciation in allopatry (Kozak & Wiens 2006). When environmental conditions change, they can form new barriers between populations of a species. The conserved niche of the species hence can become the reason for population isolation and emergence of distinct genetic lineages (Peterson et al. 1999; Martínez-Meyer et al. 2004; Mairal et al. 2017). If niches are conserved, the geographical overlap of sister species could provide clues about its mode of divergence. Immediately, sympatric divergence should produce distributions that overlap considerably, whereas allopatric divergence not (Nakazato et al. 2010). However, these patterns are very hard to study, since sister species are subject to range changes after speciation, and can coexist in sympatry after allopatric speciation, or the opposite (Nakazato et al. 2010). Sister species are also known to diverge due to ecological adaptation but still maintain some parapatric geographical overlap (and gene flow) in ecotone areas (Tarroso et al. 2014).

1.1.3 Species coexistence and spatial richness patterns

Besides the discussion of how ecological niches shape distributions and speciation, it is relevant to observe that some areas have higher species richness, and can better host species of partially overlapping niches (Palmer 1994). The drivers of this species richness patterns are related with topo-climatic, historical and biological factors like primary productivity (Rosenzweig & Abramsky 1993; Stevens & Carson 2002; Hurlbert & Stegen 2014), but the mechanisms regulating such interactions are poorly understood

(Hawkins et al. 2003). One of the main patterns of species richness, even though not universal, is that species richness peaks at intermediate levels of primary productivity (Graham & Duda 2011; Fraser et al. 2015). At low productivity level, few species can tolerate the environmental stress, competition and lack of resources. At high productivity a few highly competitive species are able to become dominant (Fraser et al. 2015). Exceptionally, some taxonomical groups diversify more in low productivity ecosystems, as reptiles in deserts (Hawkins et al. 2003), which highlights the idea that species richness patterns are dependent on region and on functional groups considered (Waide et al. 1999).

Two opposing groups of theories explain the coexistence of similar species. On the one hand, the established niche theories assume adaptive evolution and point to minimum niche differentiation as the main reason for species to coexist, through reduced interspecific competition (Silvertown 2004). In that light, species richness is induced by environmental variability that provides distinct opportunities (e.g. habitats) for more species with different niches (Turelli 1978). However, if species niches overlap partially, the small effects of competition with many species can be equivalent to strong competition with one species (see "diffuse competition" in Pianka 1974). As such, a very high environmental variability might not correspond to a very high species diversity. On the other hand, the Unified Neutral Theory of Biodiversity and Evolution (Hubbell 2001) ignores niche differences at all, and attributes the causes of species distributions and coexistence to stochastic population dynamics (Gaston & Chown 2005). Even though this theory can predict some patterns of diversity and distribution (Volkov et al. 2003), it has been generally regarded as a null hypothesis against niche theory (Gaston & Chown 2005). Efforts have been made to integrate both theories into one, the continuum hypothesis (Gravel et al. 2006). This hypothesis states that species distributions are defined by ecological niches, but that the tendency for competitive exclusion is counter-balanced by continuous immigration and stochastical processes (Gravel et al. 2006). But to what extent are stochastical processes relevant compared with ecological niches and environmental constraints? The latest studies resolve the discussion with geographical scale (Chase 2014), implying that broader scales of analysis (e.g. continental) reveal high importance of niches and environmental factors, while smaller scales (e.g. local level, the level of a protected area of 100 km^2) highlight more stochastic factors (Legendre et al. 2009; Garzon-Lopez et al. 2014; Chase 2014). Consequently, benign climate and higher primary productivity levels should be predictors of high species richness at continental scales, while environmental variability and stochastic population

dynamics should take a higher importance at local levels (Chase & Knight 2013). Thus, when comparing species distributions and analyzing species richness, it is very relevant to consider the same scale of analysis for every species (Rahbek 2005; Chase & Knight 2013; Chase 2014). Overall in biogeography studies, climatic factors appear to be most relevant influencing species distributions at global and continental scales, while topography and land cover can show stronger effects at regional and local scales (Pearson & Dawson 2003). However, the weight of environmental variables can be fundamentally different between regions and groups of taxa. For example, ectotherms and endotherms react differently when concerning primary productivity (PP) and temperature variables (Buckley et al. 2012). Oppositely to ectotherms, endotherm distributions and species richness seem to be more driven by primary productivity than temperature variables, which can be explained by fundamental differences in the physiology of these organisms (Buckley et al. 2012).

1.2 Approaches

There are two main approaches in ecological modeling. Mechanistic modeling is based on knowledge of the biological constraints of species, calibrated with observations in controlled field or laboratory studies (Morin & Thuiller 2009). This kind of modeling can partially infer the fundamental niche of species, since it is based on pure reactions to the environment (Kearney & Porter 2009). Correlative modeling uses geographically recorded presences and absences to infer statistically the niche of species and corresponding environmental constraints. Correlative modeling can infer the realized niche of species, by considering real locations where the species is present or absent due to factors as competition and historical/current dispersal barriers (Holt 2003). Correlative ENM have become a standard approach to study species distributions, especially in remote areas, since it doesn't always require elaborated experimental designs to infer realized niches that resemble the real distribution of the species (Merow et al. 2016). Acknowledging the strength and relevance of correlative modeling, it is true that it can also be subject to several errors and pitfalls. These methods assume random/representative sampling and constant detection probability, which are rarely met (Yackulic et al. 2013). Frequently the information on species occurrence proves biased and incomplete undermining models or inflating accuracy measures (e.g.Veloz 2009; Martínez-Freiría et al. 2016). An example of a known issue is sample size affecting the results by affecting the number of test-training samples (Stockwell & Peterson 2002). The spatial extent of analysis can also affect the results, creating overfitted models

(VanDerWal et al. 2009), especially for small range species (or specialized in micro-habitats) (Guisan et al., 2006). As solutions there are many decisions on the modeling method and settings to apply that are essential to the outcome and reliability of the model (Elith et al. 2006; Merow et al. 2013). Recently were created hybrid modelling approaches that consider both correlative and mechanistic models and seem to perform better. These new approaches perform correlative models and posteriorly calibrate them with some biological trait, as population dynamics and dispersal (Fordham et al. 2013; Fordham et al. 2014). They could become standard practice in the future, provided there is data on biological traits of the species to study (Fordham et al. 2014).

There are essentially two kinds of Correlative Ecological Niche-based Models (ENMs): presence and absence ENMs and presence-only ENMs (Brotons et al. 2004; Elith et al. 2006). Having both presence and absence data greatly increases the accuracy of ecological modeling (Elith et al. 2006). If representative, presence and absence ENMs are viewed as an unbiased description of the realized niche of the species (Smith 2013). However, it is hard to be sure of real absence of a species in a given place, since it may exist there but simply might not be found by researchers (MacKenzie 2005). This holds true especially for rare or low detectability species (Lahoz-Monfort et al. 2014). In most cases, only presence information can be gathered from opportunistic sampling and museum collections (Graham et al. 2004). Absence data are especially unavailable for vast and undersampled regions where modeling can prove very relevant (Soberon 1999). For these reasons presence-only methods are very important and common in current research (Elith et al. 2006). Most common presence and absence ENMs are Generalized Linear Models and Generalized Additive Models, with a robust statistical basis and ability to realistically model ecological relationships (Austin 2002). As for presence-only ENMs, Maxent method has proved the most useful for small data sets, where it outperforms other methods (Elith et al. 2006). The Maxent algorithm is based on the maximum entropy theory (Phillips et al. 2006) and has the big advantage of being less sensitive to the choice of calibration area for background data (Giovanelli et al. 2010). Maxent performs particularly well with small sample sizes (<20) and with taxa that have small distributions (Phillips et al. 2006; Elith et al. 2006; Hernandez et al. 2006) but is sensible to geographically biased sampling (Merow et al. 2013).

1.3 North Africa

In spite of big efforts to study biodiversity there is yet much to uncover, particularly in remote areas (Strange et al. 2007). Many of these areas have lodged long term human conflicts and civil unrest, effectively repelling scientists (Strange et al. 2007) and only allowing sporadic species explorations (Rebelo & Brito 2007). The results are incomplete distribution maps, represented by continuous polygons in the IUCN dataset (www.iucn.org). Deserts, also because they have lower species richness and abundance, have often been forgotten when considering biodiversity research and conservation (Durant et al. 2012). Notwithstanding, deserts present high percentages of endemic species which are among the most vulnerable to climate changes due to extreme environments they inhabit (Vale & Brito 2015). Even in deserts there are increasing anthropogenic pressures such as mining and construction of roads, damaging natural environments of the species (Root et al. 2003). It is important to study the biodiversity of deserts in order to try to protect it in the future.

North Africa stands out as a very interesting area to study biodiversity, having extreme conditions and highly adapted life forms (Brito et al. 2011). The most obvious feature of the region is the Sahara Desert, the largest hot desert in the world. Along the desert southern borders is the Sahel, a semi-arid region that makes a transition to the African savannah (Huber et al. 2011). To the north of the desert it is located the Mediterranean region, which includes one of the world's biodiversity hotspots (Myers et al. 2000). Even though generally viewed as just a homogenous arid area, the Sahara has been pointed out for its topographical and climatic diversity, having steep environmental gradients, mountains and local hotspots of biodiversity (Brito et al. 2014). The existing steep environmental gradients emerge from the transition from Mediterranean to Tropical climate influences (Le Houerou 1997) and also correspond to the transition between Palearctic and Afro-tropical biogeographical realms (Olson et al. 2001). These two realms have very distinct fauna and flora that admixture in North Africa (Le Houerou 1992; Brito et al. 2016). The Sahara desert has been expanding and retreating throughout the last 6 million years following climatic shifts (Le Houerou 1992; Le Houerou 1997) to which species responded in variable ways. During humid periods range expansions are thought to have occurred for mesic species and range contractions for xeric species, while opposite is expected during arid periods (Le Houerou 1997; Brito et al. 2014). The humid periods are thought to have hosted rivers, lakes and vast savannahs (Kröpelin et al. 2008) but the discussion of how much water they received is still open (Coulthard et al. 2013; Tierney & Pausata 2017). The last climatic shift seems

to have occurred around 7000 years ago leading to the aridity seen today (Gasse 2000; Kröpelin et al. 2008; Tierney & Pausata 2017). In the present day climate the distribution of biodiversity varies along the existing gradients of environmental variables (Le Houerou 1997). Since this is an arid area biodiversity is especially limited by the presence of water, either in the form of precipitation, air humidity, rivers, lakes or water pools (Brito et al. 2014; Żmudzka et al. 2014). Overall, there is an increasing gradient of precipitation from the desert areas to the north reaching the Mediterranean sea and to the south until reaching Sahel and savannah areas (Sayre et al. 2013). There are also regional variations related to proximity to the Atlantic ocean and mountain ranges (Campos et al. 2012). Proximity to the ocean brings smaller amplitudes of temperature and more humidity, with precipitation or fog, while high altitude tends to bring lower temperatures and more precipitation (Hijmans et al., 2005). With such mild characteristics the Atlantic coastal area is hypothesized to act as a corridor of biodiversity between the Palearctic and Afrotropical realms (Fig. 1; Brito et al., 2009, 2011, 2014).

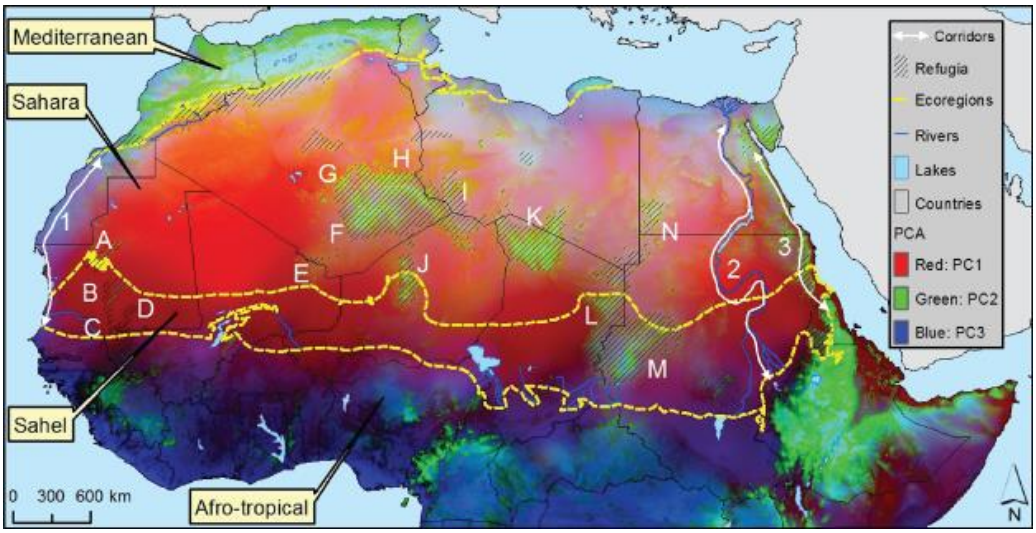

Fig. 1. Environmental variability in North Africa derived by spatial principal components analysis (SPCA), approximate boundaries between groups of ecoregions in yellow (Olson et al. 2001), hypothesized dispersal corridors (1. Atlantic Sahara; 2. Nile River; 3. Red Sea Sahara) and biodiversity refugia across the Sahara-Sahel (A-N). Composite map of SPCA, where PC1 (44.0%): annual precipitation, precipitation of wettest month, and temperature annual range; PC2 (33.4%): altitude, annual mean temperature, and minimum temperature of coldest month; and PC3 (9.4%): topography roughness index. Environmental factors from Worldclim database (www.worldclim.org) at 2.5 arc-second resolution. After: (Brito et al. 2014).

Gradually, the biogeography and ecology in North Africa start to be deciphered (Brito et al. 2014). A good example of a biogeographic study in the region tackles canids (Brito et al. 2009). It identifies distinguishable biogeographic patterns, with either Saharan, Peri-Saharan or Sahelian affinities, and highlights the biological value of the Saharan mountains, as they constitute suitable areas for all studied species. Many following studies suggested the importance of mountains as climate refugia and allopatric speciation nurseries (Brito et al. 2014). Allopatric, parapatric and sympatric speciation

modes are hard to distinguish, especially in climatically dynamic regions were species repeatedly change ranges. There is a high amount of cryptic diversity in North Africa that might cause scientists to fail to recognize accurately the current distribution patterns (Brito et al. 2014). The emergence of lower cost molecular methodologies, as DNA barcoding with one or a few reference genes (Stoeckle 2003), has brought fresh information and the promise to resolve the taxonomy of the region (Barata et al. 2012). As illustration is the recent description of the cryptic African Wolf, *Canis anthus*, previously thought to be part of the Golden-Jackal species (Gaubert et al. 2012; Koepfli et al. 2015). A species like the jackal is subject to higher attention both by researchers and authorities, but many less charismatic groups of animals remain less studied (Sitas et al. 2009). In the end, biodiversity is composed by many species, and not just the charismatic ones. One of the groups of animals with less solved taxonomy and biodiversity patterns in North Africa is rodents, for which the existing doubts are finally being tackled with molecular techniques (Ndiaye et al. 2012, 2014). Only using correct taxonomic information and species identification it is possible to study the ecological niches of species and their distribution.

1.4 Gerbillus Genus

The *Gerbillus* genus (*Muridae* family) is one of the most species rich among rodents, with more than 50 currently recognized species ranging from North Africa to India (Musser & Carleton 2005). Gerbils show remarkable adaptations to water scarcity (Burns & Balekjian 1956; Khalil & Tawfic 1963) and can occur in very extreme arid conditions. In fact, they have been suggested as indicators of desertification in the sub-Sahara, where they colonize areas of increasing aridification (Duplantier et al. 1991; Thiam et al. 2008). Generally, the distribution of desert rodents like *Gerbillus* is explained with vegetation, productivity and substrate type (Abramsky 1988; Traba et al. 2010; Traba et al. 2016). While vegetation can provide different foraging opportunities and cover from predators, substrate type is relevant for the capacity of constructing burrows (Torre et al. 2007) and can affect the energy efficiency of food foraging (Ziv et al. 1995). Even the substrate colour can prove relevant, by exerting pressures in different fur colours for camouflage (Boratyński et al. 2017). Desert rodents often form species assemblages characterized by a few coexisting species, exhibiting habitat and temporal segregation (Abramsky 1988; Ziv et al. 1993; Abramsky et al. 2005; Wasserberg et al. 2006). Segregation is both the result of competition and a mechanism to avoid it, where each species differently manages factors as predation risk, food availability and abiotic conditions (Kotler & Brown 1999). Some bigger and more aggressive species, as *G.*

pyramidum, can exhibit dominance over others, driving them to sub-optimal temporal and habitat foraging (Ziv et al. 1993). Smaller species can better avoid predators or be more efficient foragers, wasting less energy in their activity, in order to survive in poor conditions (Ziv et al. 1993). For example, although with a very limited sample size, Traba et al. (2016) observed that *G. tarabuli* and *G. campestris* preferred habitats with sandy soils whilst the *G. amoenus* and *G. gerbillus* appeared to also be present in less favorable rocky habitats. Both later species are small in size and appear to minimize predation risk by segregating to areas with shrub cover (Traba et al. 2016). It has also been shown that the small *G. henleyi* is often excluded from productive sandy desert habitats by bigger *G. pyramidum* (Abramsky et al. 2005). In terms of temporal segregation *G. andersoni* was hipothesised to be active very early in the night, before the dominant *G. pyramidum* become active and when predators are more active as well (Ziv et al. 1993). *Gerbillus andersoni* has also been recorded to be active late in the night when *G. pyramidum* is not active anymore (Wasserberg et al. 2006). In the beginning of the night, the smaller species is trading off security from predators in order to access richer resources before it is excluded by the dominant species (Ziv et al. 1993). In the end of the night, the smaller species is trading off resource availability for a less competitive environment. Above examples show that gerbils are a very ecologically interesting study group, distributing the entire North Africa, presenting a high number of species, several of which co-exist in poor resource areas, and probably exploring slightly different niches.

The phylogeny of the *Gerbillus* genus has been recently revised in Northwestern Africa (Fig. 2; Ndiaye et al. 2012, 2016), estimating the emergence of the genus to 3.60–6.81 Myr ago (Ndiaye et al. 2012). Thus, the emergence of this genus corresponds to the upper Pliocene and early Pleistocene, periods characterized by gradual climatic cooling and aridification in Northern Africa (deMenocal 2004). Many divergence events within the genera are dated to later periods, during the Pleistocene (Ndiaye et al. 2012), when strong climatic changes would be translated in shifts between arid and humid periods (Gasse 2000; Kröpelin et al. 2008). It is also in the Pleistocene during the interglacial periods that marine transgressions are known to have systematically occurred along the North Atlantic coast of Africa (Weisrock 2012) and are hypothesized to be responsible for several allopatric divergence events of gerbils (Lay 1983; Ndiaye et al. 2012). Even at an intra-specific level the Atlantic Coast of North Africa seems to host a high level of genetic differentiation as noticed by Nicolas et al. (2014) studying the genetic structure of *G. campestris*.

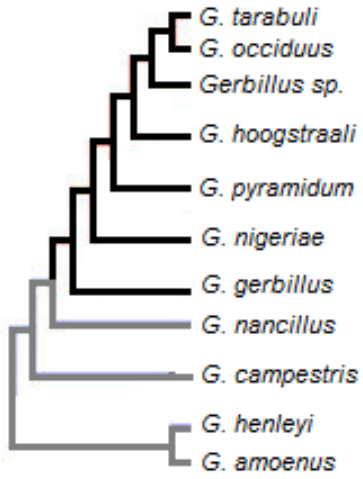

Fig. 2. Phylogeny of the *Gerbillus* genus in North-West Africa based on cytochrome b sequences. Branches in grey don't have resolved nodes with statistical support (Ndiaye et al. 2016). After Ndiaye et al. (2016).

Ultimately, Northwestern Africa is a very interesting study area for *Gerbillus* with surprising and unexplained species richness. The area hosts endemic species with very small ranges (less than 300 km^2) like *G. hesperinus*, *G. hoogstrali*, *G. occiduus* (Musser & Carleton 2005), as well as an undescribed new species, *Gerbillus sp.* (Ndiaye et al. 2012). Other species in the region have wide North African ranges (more than 3000 km^2): *G. amoenus*, *G. tarabuli*, *G. gerbillus, G. henleyi* and *G. campestris* (Granjon 2016;. Granjon 2016a; Aulagnier & Granjon 2016). Finally, in the south there are species like *G. nigeriae* and *G. nancillus*, occupying the Sahel (Granjon 2016c; Schlitter & Granjon 2008). Some of *Gerbillus* seem to have stronger affinities for the desert, while others seem to have strong affinities for its periphery, for the coast of Atlantic or for the Sahel. Yet, the ecological niches and ecological/environmental mechanisms promoting the species richness of gerbils in Northwestern Africa are yet unexplored.

2 Aims, hypothesis and predictions

The main aim of this thesis was to unveil biogeographical patterns of the *Gerbillus* genus by compiling the knowledge on the distributions of all species that exist on the Atlantic coast of Northwestern Africa: *G. amoenus*, *G. campestris, G. gerbillus, G. henleyi, G. hesperinus, G. hoogstraali, G. nancillus, G. nigeriae, G. occiduus, G. pyramidum, Gerbillus sp., G. tarabuli.* It was the aim of this thesis to evaluate the topo-climatic and habitat constraints to the distributions of the studied species and estimate those distributions under past climatic scenarios. Finally, this thesis should predict spatial species richness for the genus and compare niches between species in the light of the niche conservatism theory (Peterson et al. 1999; Kozak & Wiens 2006; Warren et al. 2008; Glor & Warren 2011).

Clearly the best solution for upgrading the biogeographical knowledge of Northern Africa has to be accomplished by intensive and accurate sampling (Guisan & Thuiller 2005). In the region, where sampling is reduced and taxonomy was unclear, some of the simplest questions remain unanswered, as for instance: What are the distributions of species? What are the ecological drivers to those distributions? How did ecological drivers change through time? And which areas host more species? This thesis provides some answers concerning the genus *Gerbillus* for which sporadic sampling was done during the last decades that aided with molecular barcoding for species differentiation (Ndiaye et al. 2016). The outline of the thesis follows several hypotheses listed below.

The first hypothesis predicts that the distributions of the considered gerbils are constrained by topo-climatic and habitat factors. The ecological niche models should highlight areas where the species are described to exist (in IUCN maps as well as new areas where novel observations were made). The models can also highlight other isolated areas, away from the know distribution of species, which would mean that the species could exist there, but it doesn't due to ecological vicariance (Kozak & Wiens 2006; Mairal et al. 2017). For example, *G. nancillus* is described to exist in only the Sahel. The model for *G. nancillus* should roughly highlight the sahel as a suitable area. The model of *G. nancillus* could also highlight some areas of the mediterranean coast as suitable. Alternatively, the distributions could be affected only by physical barriers, biotic interactions and stochastical population dynamics, as described by the Unified Neutral Theory of Biodiversity and Evolution (Hubbell 2001), and the ENM would not resemble their real distributions. Returning to the example of *G. nancillus*, the model could highlight wide areas of the Sahara and north Atlantic coast, where the species

does not occur. In the alternative hypothesis, the models of species with very different distributions could be very similar.

Since most *Gerbillus* are adapted to arid conditions the second hypothesis predicts that species distributions would be negatively affected (distribution ranges would shrink) in past humid climatic stages of Sahara, as during the Middle-Holocene (Le Houerou 1992). In more humid climate scenarios the prediction is that the species from the Atlantic Sahara or the Sahel would have been less negatively affected than species that exist in the most arid conditions of the Sahara. Alternatively, all or some *Gerbillus* species could have the level of plasticity to persist in more humid conditions or not be affected by precipitation changes at all.

A third hypothesis explored here is related with species richness of the genus in Northwestern Africa. Higher species richness should theoretically be found in ecoregions of milder climates and intermediate primary productivity (Graham & Duda 2011). Overlapping models of environmental suitability for all species will show areas of higher potential species richness. The prediction is that these areas will correspond to the climatically mild Atlantic coast, as well as to areas of intermediate precipitation (and primary productivity) in north of the Sahel and south of Mediterranean habitats. Alternatively, areas with higher potential species richness could have extreme climates or very low primary productivity, which would highlight the considered species as only thriving in extreme conditions, where competition is lower.

The fourth hypothesis of this study predicts that the niches of the considered *Gerbillus* are similar as a result of niche conservatism (Peterson et al. 1999; Warren et al. 2008). If existing, niche differences should be found between species with higher phylogenetic distances, e.g. between *G. amoenus* and *G. tarabuli* (Fig. 2). This hypothesis would suggest past/present geographical barriers as main mechanisms of speciation (Peterson et al. 1999; Warren et al. 2008). Alternatively, niche overlap might correspond to geographical overlap (Graham et al. 2004), indicating niche differences between species that have very different distributions, e.g. between coastal and sahelian species. The alternative hypothesis would suggest ecological adaptation as the main cause for niche overlap.

Even though the considered study area is North Africa, the focus of this work is on its western part where the taxonomy for the *Gerbillus* genus has recently become more clear (Ndiaye et al. 2012, 2016). Moreover, the western part of North Africa is one of the most interesting areas to evaluate species richness and niche overlap between species.

The area is interesting due to the its sharp environmental gradients constraining species (Brito et al. 2014) and a supposedly turbulent history, with marine transgressions (Weisrock 2012) and climatic oscillations (Le Houerou 1997; Foley et al. 2003; Kröpelin et al. 2008) supposedly promoting vicariant processes. The intention of this thesis is to explore the role of the Atlantic Sahara as a corridor for biodiversity and a region prone for diversification events. All patterns explored here can be useful to understand better the distributions and history of *Gerbillus* in Northwestern Africa. Indeed, they can also be extrapolated as an example of how biodiversity is structured in the area.

3 Methods

3.1 Species and observation data

Twelve *Gerbillus* species, and 444 species locations (Supplementary material TableS1), present in Northwestern Africa were used in this study (Table 1). From these locations 150 were extracted from recent publications (Ndiaye et al. 2012, 2013, 2014, 2016; Nicolas et al. 2014; Boratyński et al. 2017) and 130 are the result of recent field work by the Biodeserts group (Supplementary material Table S1). Biodeserts develops scientific research in desert, arid and semi-arid regions, with emphasis in North Africa and the Mediterranean Basin. I participated in two expeditions to North Africa. The first to Morocco, Mauritania and Mali in 2014 and the second to Morocco in 2016 (Guerreiro et al. 2016). Specimens were captured by live-trapping with hand nets or baited Sherman traps, a standard method for small mammal surveys (Hoffmann et al. 2010). Body measurements and photographs from captured individuals were taken for species identification. The animals were released after tissue sample collection (pieces of ears collected for genetic studies). Additionally, tissue samples were collected from found dead animals. All samples coordinates were registered with a precise GPS system.

Table 1. Studied species and number of samples/locations, depicting the number of samples confirmed by molecular analyses.

Species	Samples	Molecular confirmation	Species	Samples	Molecular confirmation
G. amoenus	48	37	*G. nancillus*	18	18
G. campestris	103	62	*G. nigeriae*	22	22
G. gerbillus	89	56	*G. occiduus*	13	13
G. henleyi	19	19	*G. pyramidum*	69	39
G. hesperinus	1	1	*Gerbillus sp.*	6	6
G. hoogstraali	1	1	*G. tarabuli*	75	68

A total of 342 specimens had molecular confirmation at the time of this research, used for species identification in a separate study (Supplementary material TableS1; Boratyński et al. 2017). This was done with barcoding, sequencing the mitochondrial cytochrome b (cyt b) gene of tissue samples (Ndiaye et al. 2016). Recent studies in *Gerbillus* systematics point out this gene as informative in differentiating species (Abiadh et al. 2010; Chevret and Dobigny 2005; Ndiaye et al., 2012, 2013). The 92 non-barcoded samples (Supplementary material TableS1) were identified using photographs, morphological features and measurements. The confidence in the species identification

of non-barcoded specimens is very high since it was carried out by experts in the field (Kowalski & Rzebik-Kowalska 1991; Granjon et al. 2002), often in species-poor areas where it is easy to distinguish the few existing species. Also, groups of samples were usually obtained by the same expert in the same region, and in those cases at least some tissue samples were barcoded confirming correct method of species identification (Ndiaye et al. 2016).

For convenience of reading, species were grouped according with distribution types. Wide distribution species are *G. amoenus, G. campestris, G. gerbillus, G. pyramidum* and *G. tarabuli*. Coastal species are *G. hesperinus, G. hoogstraali, G. occiduus* and *Gerbillus sp*.. Sahelien species are *G. nancillus* and *G. nigeriae. Gerbillus henleyi* was not assigned to any group, but is often compared with the sahelian species.

3.2 Study area and data treatment

All data in this study was projected with GCS WGS 1984 coordinate system datum. The pixel size of the analysis was 5x5 km (2.5 arc minutes). A coarser pixel size was preferred since part of the observations in literature come from natural history collections, which often have significant error in coordinates (Graham et al. 2004). All species were treated with the same scale of study area and pixel size to avoid false comparisons (Rahbek 2005). The study area was defined as all continental area within a buffer of 200 kilometers around the minimum polygon encompassing all field observations (minimum bounding geometry, ESRI 2014). This study area should comprise all possible regions occupied by the studied species, apart from *G. henleyi*, which is described to exist in the coast of the Arabian Peninsula (Supplementary material Fig. S1; Granjon 2016b). The study area encompasses the whole North Africa (and the Sinai Peninsula), and extends to the south until Senegal and Gambia in the west and Sudan in the East (Fig. 3).

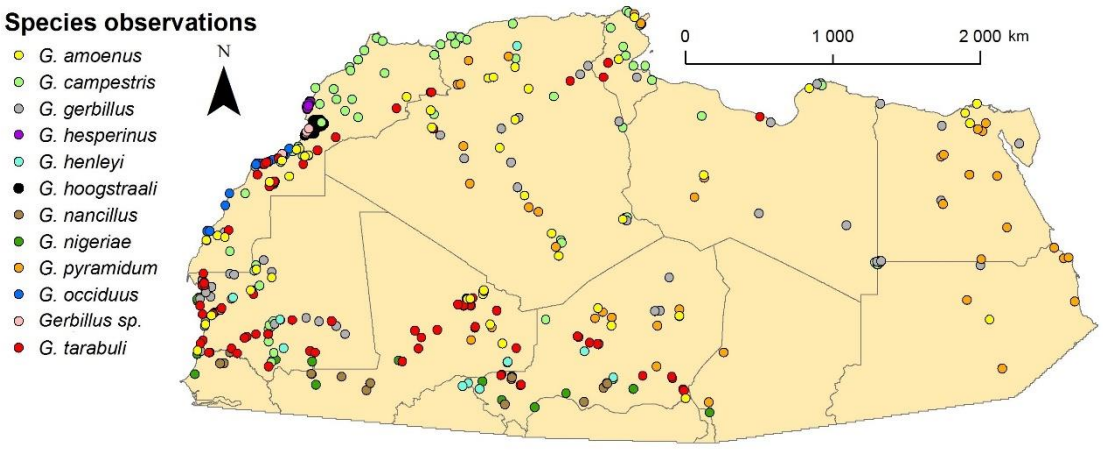

Fig. 3. Study area and species observations (including generated points for *G. hoogstraali* and *G. hesperinus*)

Lack of a priori designed balanced sampling design creates problems of spatial autocorrelation between presence points (Veloz 2009). This happens due to biases in sampling effort, which can affect ecological niche models (Merow et al. 2013). A first view on the distribution of samples leads to the conclusion that some areas are clearly undersampled or not sampled at all, as is the case of Chad, Sudan, Egypt and Lybia, as well as the interior of Mauritania, north west Mali and large areas of Algeria. Most of these regions have issues with accessibility, safety and armed conflicts (Brito et al. 2014). Spatial filtering of occurrence records has been demonstrated to be one of the best solutions to account for sampling bias (Kramer-Schadt et al. 2013), and was implemented here by eliminating same species observations inside the same 5x5 km cells of a grid, created with the Create Fishnet tool of ArcGIS (e.g. Martínez-Freiría et al. 2015; Vale et al. 2016). The degree of data clustering was verified a priori and a posteriori with the Average Nearest Neighbor tool of ArcGIS, confirming small decreases in clustering (Supplementary material Table S2) but retaining clustered distributions (except for: *G. henleyi, G. nigeriae* and the coastal species which presented random or dispersed sample distributions). Clustered distributions of observations are known to decrease model accuracy (Phillips et al. 2009; Kramer-Schadt et al. 2013; Syfert et al. 2013). Yet, as reducing data clustering any further would force the reduction important presence records, the decision was to progress with 5x5 km filtered data.

The two species *G. hesperinus* and *G. hoogstraali* presented a small sample size to conduct ecological modeling (Elith et al. 2011) and therefore additional random points were created for them using their IUCN distribution maps and the “create random points” tool of ArcMap (ESRI 2014). The same happened with *Gerbillus sp*., for which was impossible to generate random points, since this new species doesn’t have a distribution map in the IUCN dataset yet. Consequently, and fully aware of the flaws of this method, four additional points were created manually, adjacent to pixels were the species was found. Including this species was an exercise of learning, to investigate how much the estimated niche for new species deviates from other species. To try to avoid problems of overfitting the models for coastal species with a very large study area (VanDerWal et al. 2009), smaller areas were defined on the coast to train these models (Supplementary material Fig. S25). These coastal areas were created with buffers of 100 kilometers around each species observations (Supplementary material Fig. S25). This method was abandoned when the results showed unrealistic projections to the whole North Africa, and the final models were trained with the first study area (Supplementary material Fig. S25).

3.3 Topo-climatic and habitat variables

To proceed to Ecological Niche-based Modeling 19 Bioclimatic variables of current climate conditions, as well as correspondent reconstructions for Middle Holocene (MH), Last Glacial Maximum (LGM) and Last Interglacial (LIG) were downloaded from Worldclim (www.worldclim.com; Hijmans et al. 2005). All variables had a pixel size of 2.5 arc minutes (~ 5x5 km). As there are several climate reconstruction scenarios for MH and LGM, 3 sources were considered for both: CCSM4 (Gent et al. 2011), MIROC-ESM (Watanabe et al. 2011) and MPI-ESM-P (Giorgetta et al. 2013). Altitude was also downloaded from the same site (2.5 arc minutes) and was used to derive slope with the "slope" function of ArcMap (ESRI 2014;Table 3). All variables were cut to the study area with the study area polygon, using the "extract by mask tool". The climatic variables were all stretched to the same range with the "statistics tool" from the Geomorphometry and Gradient metrics toolbox (Evans et al. 2014) and then tested for correlations (Pearson correlation; Supplementary material Table S3), using Band Collection Statistics tool of ArcMap (Kramer-Schadt et al. 2013; ESRI 2014). A set of seven variables (Table 2) was chosen avoiding all high correlations (R>0.7; Supplementary material Table S3).

Table 2. Chosen set of uncorrelated bioclimatic variables (|R|<0.70).

Code	Bioclimatic variable	Range Units
Bio2	Mean diurnal range (Mean of monthly x (max temp - min temp))	5.9-20.8 ºC
Bio5	Max temperature of warmest month	22.6-48.9 ºC
Bio6	Min temperature of coldest month	-12.4-18.9 ºC
Bio7	Temperature annual range (P5-P6)	12.4-42.8 ºC
Bio16	Mean precipitation of wettest quarter	0-787 mm
Bio17	Mean precipitation of driest quarter (Eliminated later)	0-85 mm
Bio19	Mean precipitation of coldest quarter	0-728 mm

Table 3 Topographical variables used in this thesis.

Code	Topographic variable	Range Units
Alt	Altitude	-129 —3688 m
Slop	Slope	0 — 13956

In addition, a land cover map was downloaded at 30 arc seconds (~1x1 km) from Globcover (publicly available at: www.postel.mediasfrance.org; GLC, 2003). This map was used to extract 16 land cover traits (Table 4). These traits were transformed to 5x5 km resolution with “aggregate” function of ArcMap, counting the percentage of pixels 1x1 km pixels inside each new 5x5 pixel (ESRI 2014). Four of these traits, related with forest habitats, were eliminated due to not being significantly represented in the study area, having lower than 1 % coverage.

Table 4. Land cover traits used in this thesis. Downloaded from Globcover (GLC, 2003)

CODE	Variable name
LC01_CROP	Croplands
LC02_CRVE	Mosaic cropland (50-70%) /vegetation (20-50%)
LC03_VECR	Mosaic vegetation (50-70%) / cropland (20-50%)
LC08_FOGR	Mosaic forest or shrubland / grassland
LC09_COSH	Closed to open (>15%) (broadleaved or needleleaved, evergreen or deciduous) shrubland (<5m)
LC10_COHE	Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses)
LC11_OPGR	Open (15-40%) grassland
LC12_SPVG	Sparse (<15%) vegetation or grassland
LC13_FBWV	Freshwater or brackish water vegetation
LC14_BARE	Bare áreas
LC15_ROCK	Consolidated bare areas (hardpans, gravels, bare rock, stones, boulders)
LC16_SAND	Non-consolidated bare areas (sandy desert)

3.4 Species distribution along environmental gradients

In order to visualize the environmental variability of the study area, two separate Principal Component Analysis (PCAs) were performed. Principal Component Analysis is a mathematical method to transform multidimensional data into a few main axis of variation (Pearson 1901). The PCAs were performed with “Principal Components” tool of ArcMap (ESRI 2014). The environmental variability of the study area was extracted from the main two axis of the Topo-climatic and Habitat PCAs by using the “sample” tool ArcMap (ESRI 2014). The environmental values corresponding to the sample points of each species were extracted with “extract values to table” tool of Arc map using each species points and both PCAs. The values for each species observations were plotted against the environmental variability using R (R Development Core Team 2013).

3.5 Ecological niche modeling of climatic data, projections to the past climate and stable climatic areas

Climate is expected to have a preponderant effect in shaping species distributions (Pearson & Dawson 2003). As so, the bulk of this thesis depends on modelling the species presences with climatic data. Since absences were impossible to obtain in the study area, a correlative presence-only method was applied to the gathered observations. Ecological models were developed with Maxent 3.3.3 (Phillips et al. 2006), a machine learning algorithm that has been consistently used to model under-sampled species distributions, as it performs well with sparse or noisy data (Phillips et al. 2006), even though it has subjective thresholds for transformation in binary presence-absence maps (Elith et al. 2006). Maxent estimates distribution probabilities by finding the probability distribution of maximum entropy (that is most spread out, or closest to uniform), subject to a set of environmental drivers (Phillips et al. 2006). A common threshold is the minimum training presence threshold, defined with the lowest environmental suitability where any observation was located. For more conservative results, 5 and 10 percentile training presence thresholds ignore respectively 5 or 10% of the lowest values (Cao et al. 2013).

Species records and variables were imported to Maxent, where modelling was performed with random seed and doing jackknife to measure variable importance. In order to better calibrate models (Elith et al. 2006), exploratory modeling was performed to determine the best combination features and settings to apply, taking in consideration the smoothness of the resulting receiver operating characteristic (ROC) curve and artifacts in the resulting models. The decided features were the linear, quadratic and

product features since more complex features would produce unrealistic models. The decided test percentage was 20% with 50 replicas for species with more than 20 observations, and 10% with 20 replicas for species with less than 20 observation points. After the exploratory modelling and accessing the contribution of each variable to explain the models, one variable was eliminated due to being irrelevant for the distribution of every species (Bio 17-Precipitation on the driest quarter). Bio 17 did not vary enough in the study area to make a difference for any species. Modeling was redone without this variable and projected with conditions from the present, Middle Holocene, Last Glacial Maximum and Last Interglacial. Model accuracy was assessed with the Area Under the Curve (AUC) of the Receiver Operator Characteristic (ROC), which is a single measure of discrimination ability (presence from random background, where a value of 1 = perfect prediction, 0·5 = prediction no better than random) of the models (Fielding & Bell 1997). The importance of each variable for explaining the species distribution is indicated by its average percent contribution to the models. The species response curves to the significant contributive variables were plotted to visualize the species relation to those same variables. Similar responses between species were taken as an indication of identical environmental drivers. Distinct responses between species were taken as sign of differential environmental drivers in their distributions, in what might be a reflection of divergent niches (Martínez-Freiría et al. 2008).

All the projections were displayed in ArcMap to assess visually the temporal changes in climatic suitability for the species and scenario differences in Middle Holocene and Last Glacial Maximum. At this point, the three scenarios for MH and for LGM were averaged with Raster Calculator (ESRI 2014), calculating average values for each pixel in the study area from the different scenarios. In order to avoid subjective thresholds for transformation of models in binary presence-absence (Elith et al. 2006), the “Fuzzy overlay” function of ArcMap (ESRI 2014) was applied to merge the projections of each species in different periods into a single projection, correspondent to climate stability. Fuzzy logic is capable of dealing with ambiguous information, risking decisions in face of uncertainty as humans do (Zadeh 1965). By applying the “AND” overlay type of “Fuzzy overlay” function, the lowest climate suitability values that each pixel had between all period models were brought up effectively producing a map highlighting areas with suitable climate throughout all time periods.

The projections of current climate suitability were transformed into binary maps of suitable/non-suitable with 5 per centile thresholds (Supplementary material Fig. S27), using the reclassify tool of ArcMap (ESRI 2014). This conservative threshold is useful when data is suspected to be partially inaccurate, ignoring the lowest values of suitability

which correspond to the 5% of training presence data (Cao et al. 2013). This threshold was chosen because the percentage of absolute sureness of correct identification in observations varied from 0% to 16.3% between species, averaging 5.56 %. All pixels under the thresholds of climatic suitability were defined as non-suitable and all pixels above those thresholds were defined as suitable. These binary maps were used count percentages of climate suitability inside five groups of Ecoregions (Olson et al. 2001), counting the number of presence pixels of each species in each ecoregion group (Brito et al. 2009; Sillero et al. 2009). The 5 defined groups of Ecoregions were: 1) Saharan ecoregions (except Atlantic Sahara), 2) Sahelian ecoregions, 3) Mediterranean ecoregions, 4) mountain ecoregions and 5) the Atlantic Sahara, a single Saharan ecoregion (Olson et al. 2001) that was considered separately due the hypothesis that it plays an important role in the distribution of many species.

3.6 Ecological niche modeling of Topo-climatic and Land Cover data

Not only climate is important to explain the distribution of *Gerbillus*. Habitat plays a key role in the distribution of several species in included in this study, with already described species habitat segregation (Wasserberg et al. 2006). Substrate type should be relevant for energy efficiency and burrow digging while vegetation can provide different foraging opportunities and shelter from predators (Torre et al. 2007). To account for climate and habitat in species distribution, the downloaded landcover variables were considered to use in modeling in conjunction with climatic variables. There were significant correlations between land cover and climatic variables (Supplementary material TableS3), tested with “Band Collection Statistics” of ArcMap (ESRI 2014). These correlations lead to the decision of using the 3 main axis of the topo-climatic PCA (tpcPCA) land cover PCA (habPCA) as modeling variables. This way there were only 6 variables for modelling, not risking over-parameterization (Phillips et al. 2006; Cao et al. 2013). Ecological Niche-based Modeling was carried out for every species with random seed and jackknifing to measure variable importance.

The projections of current environmental suitability were transformed into binary maps of suitable/non-suitable with 5 per centile thresholds (Supplementary material Fig. S28), using the reclassify tool of ArcMap (ESRI 2014). The binary maps were overlapped with Raster Calculator of ArcMap (ESRI 2014) to generate a single map of environmental suitability for all species, defined here as a potential species richness map.

3.7 Ecological niches – Tests of overlap, identity and background

ENMtools 1.4.4 (Warren et al. 2010) was used to evaluate the ecological niche overlap between pairs of species and to test niche conservatism between them. A simple test, the Schoener's D statistic (0 – no overlap, 1 – complete overlap), measures the overlap between two binary predictions of suitability for species (Supplementary material Fig. S27-S28; Schoener 1968; Warren et al. 2008). Afterwards, two hypothesis tests with 50 pseudo-replicates were applied. The niche identity test is set upon the niche equivalency hypothesis, asking whether the observations of pairs of species are more different than expected if they would be drawn from the same underlying distribution (Warren et al. 2008). It asks if the species niches are exactly equivalent. Niches are considered non-equivalent if the distribution of identity tests deviated from the corresponding Schoener's D overlap measure. To test niche conservatism, the background similarity test compares one species observations with the background variability of another species' ENM. It asks if species prefer similar environmental variables, even if the geographical distributions are non-overlapping (Warren et al. 2008). Background tests are also evaluated against the Schoener's D overlap measure, but they are one-tailed tests. Only if the niches overlap (Schoener's D) is lower than the distribution of background tests are the species niches considered divergent. If the niches overlap (Schoener's D) is inside or is higher than the distribution of background tests the species are considered more similar than expected. The significance of the difference between the Schoener's D overlap and the identity and background tests was determined by Mann Whitney U tests, calculated in SPSS version 24.0 (IBM 2016). Hypothesis tests with *Gerbillus sp.* had unclear distributions, probably due to the minimum number of samples used (only 10), some of which artificial. Hence, the species was not considered in this analysis.

4 Results

4.1 Species along environmental gradients

The first PCA (tpcPCA) included the set of 7 uncorrelated climatic variables, as well as altitude and slope variables. In Table 5 are depicted the Eigenvalues of the main axis of the topo-climatic PCA. The first axis (tpcPC1), explaining 49.13% of variation, was affected mainly by mean precipitation on the wettest quarter (Bio16) and temperature annual range (Bio7). The second axis (tpcPC2), explaining 27.63 % of variation, was mainly affected by minimum temperature of coldest month (Table 5) and temperature annual range (Bio7). The third axis (tpcPC3), explaining 12.25 % of variation, was mainly affected by mean precipitation on the wettest quarter (Bio16). The suggested interpretation of these axis is: tpcPC1 – Climate seasonality; tpcPC2 - Temperature extremes, tpcPC3 - Precipitation.

Table 5. Eigenvalues and loadings for the Topo-Climatic components in a Principal Component Analysis (PCA) tpcPCA. In bold are outlined the main loading values for each Principal Component.

Axis	**tpcPC1**	**tpcPC2**	**tpcPC3**
Eigen Value	49.13	27.63	12.25
Variables	**Component loading**		
Bio19	-0.05	-0.19	0.17
Bio16	**-0.57**	0.26	**0.76**
Bio7	**0.62**	0.08	0.38
Bio6	-0.38	**0.49**	-0.39
Bio5	0.27	**0.70**	-0.02
Bio2	0.26	0.37	0.16
Slop	0.00	-0.07	0.08
Alt	0.07	-0.15	0.26

The second PCA (habPCA; Table 6) included the land cover variables, and its main axis distinguished respectively: sandy bare areas from consolidated bare areas (habPC1; Table 6), consolidated bare areas from other bare areas, as salt deposits (habPC2; Table 6) and other bare areas from non-bare areas, especially croplands (habPC3; Table 6).

Table 6. Eingenvalues and loadings for the Land cover components in a Principal Component Analysis (PCA) habPCA. In bold are outlined the main loading values for each Principal Component.

Axis	habPC1	habPC2	habPC3
Eigen Value	46.25	23.62	12.88
Variables	**Component loading**		
LC01_CROP	0.00	-0.06	-0.18
LC02_CRVE	0.00	-0.05	-0.14
LC03_VECR	-0.01	-0.10	-0.33
LC08_FOGR	0.00	-0.04	-0.09
LC09_COSH	0.00	-0.02	-0.07
LC10_COHE	0.01	-0.14	-0.23
LC11_OPGR	0.00	-0.04	-0.12
LC12_SPVG	0.01	-0.09	-0.13
LC13_FBWV	0.00	0.00	-0.01
LC14_BARE	0.09	**-0.56**	**0.76**
LC15_ROCK	**0.66**	**0.63**	0.26
LC16_SAND	**-0.74**	**0.49**	0.32

Most observations were made in areas of high values of tpcPC2 and tpcPC3. Only *G. gerbillus* and *G. pyramidum* were observed in areas with simultaneously high values of tpcPC1 and tpcPC2 and low values of tpcPC3, depicted in yellow in Fig. 4.

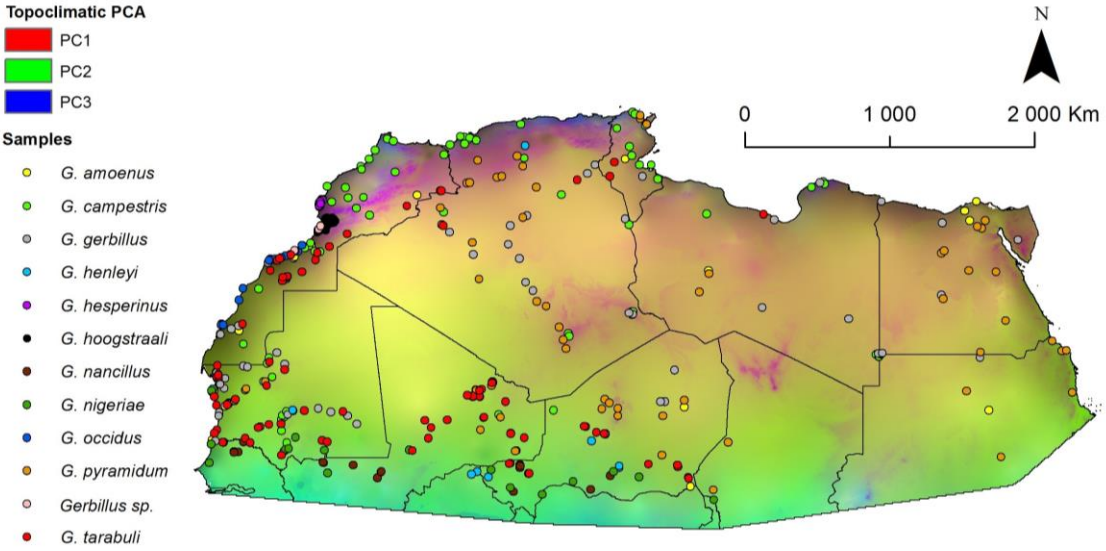

Fig. 4. Principal component analysis of the topo-climatic data in the study area (tpcPCA), with overlapping distribution of species samples. Main axis of variation in Red (49.13%), Green (27.63%) and Blue (12.25%). Axis interpretations: tpcPC1- Climate seasonality; tpcPC2- Temperature extremes, tpcPC3- Precipitation and altitude.

When plotting tpcPC1 and tpcPC2 in a graph there was segregation of species along the topo-climatic axis (Fig. 5). The coastal species occupied the low values of tpcPC1 and tpcPC2 but the sahelian species occupied intermediate values of tpcPC1 and high

values of tpcPC2. The wide distribution species occupied large part of the spectrum of variation, but avoided areas of simultaneously low values of tpcPC1 and high values of tpcPC2.

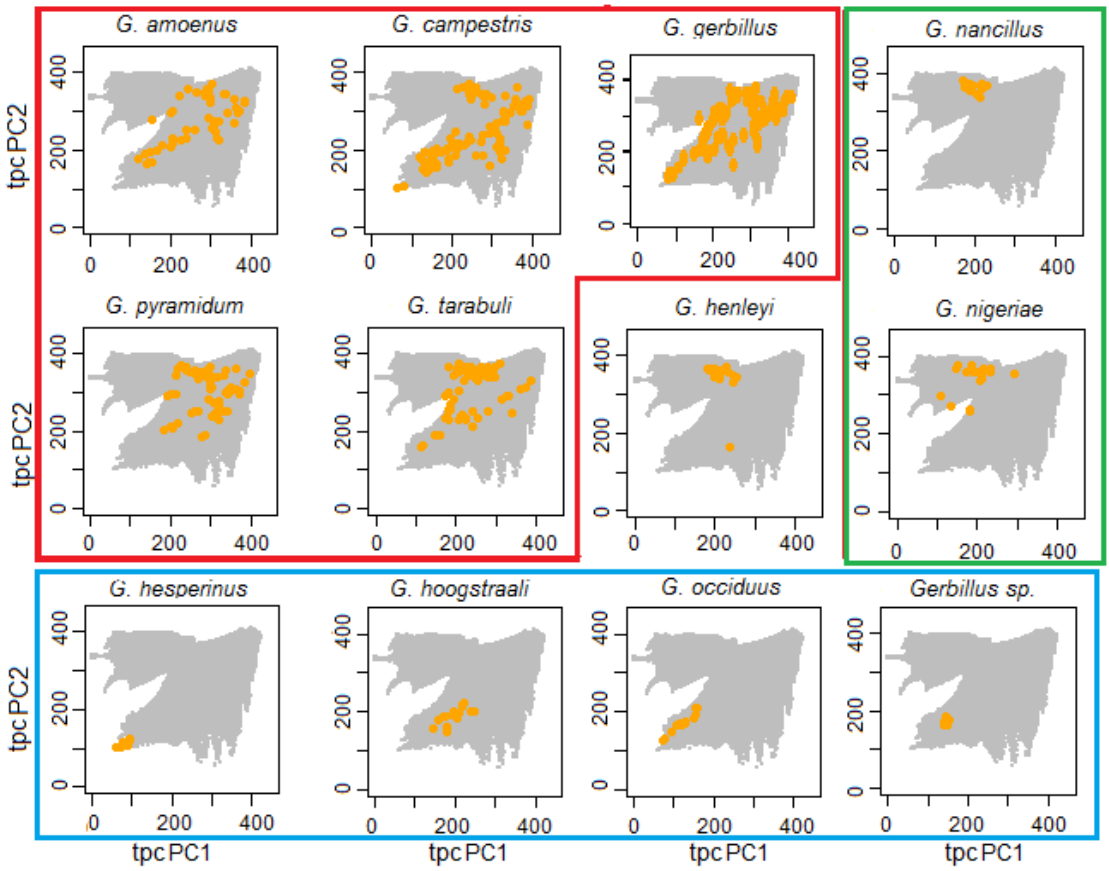

Fig. 5. Distribution of species records (orange) in relation to the topo-climatic variability of North Africa (grey points). Topo-climatic variability relates to the first two PCAs' axis (tpcPC1 and tpcPC2), explaining 75% of variance. Species are grouped per distribution types: wide distribution species (red box), coastal species (blue box) and Sahelian species (green box). *Gerbillus henleyi* does not belong to any group.

There were less observations of species in sandy desert habitats (with low values of habPC1 and intermediate values of habPC2 and habPC3), depicted in light blue in Fig. 6. Both the sahelian species and *G. campestris* were observed mainly in non-desert habitats (with intermediate values for all habPCs), depicted in brown in Fig. 6. When plotting the landcover values of observations against the background variability of habPC1 and habPC2, no clear pattern emerges (Fig. 7). All species, especially the wide distribution species, were found in multiple combinations of values of habPC1 and habPC2 (Fig. 7). *Gerbillus occiduus* was the only species that was not found in areas of low PC2.

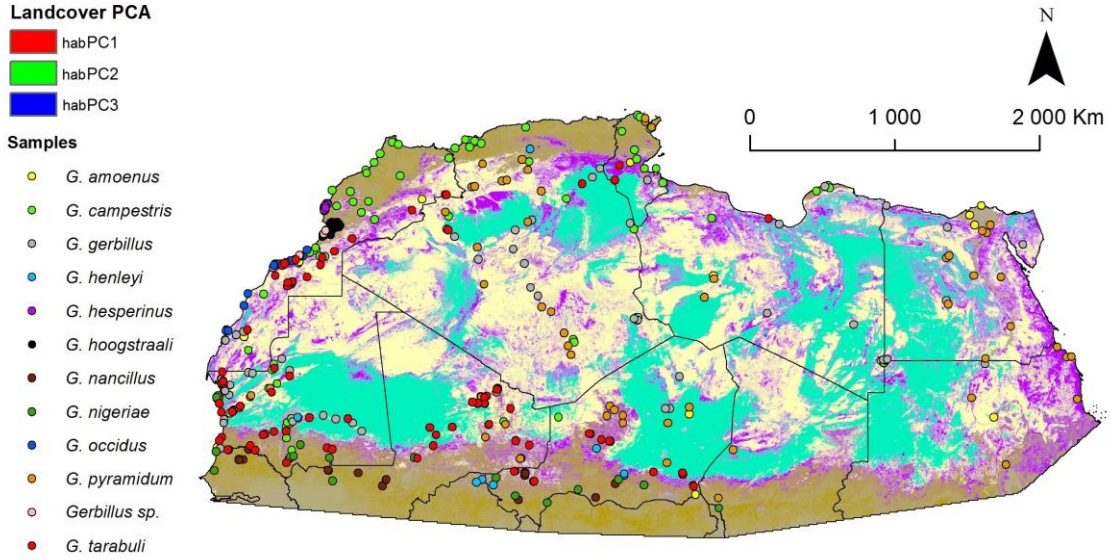

Fig. 6. Principal component analysis of the landcover data in the study area (habPCA), with overlapping distribution of species samples. Main axis of variation in Red (53.21%), Green (29.01%) and Blue (13.14%). Light blue is the result of low values of habPC1 and intermediate values of habPC2 and habPC3 and seems to correspond to sandy desert. White is the result of high values of habPC1 and habPC2 and intermediate values of habPC3 and seems to correspond to rocky desert. The brown is the result of high values of habPC3 and intermediate values of habPC1 and habPC2 and corresponds to non-desert. Purple is the result of intermediate values of habPC1, low values of habPC2 high values of habPC3 and seems to correspond to mixed habitats.

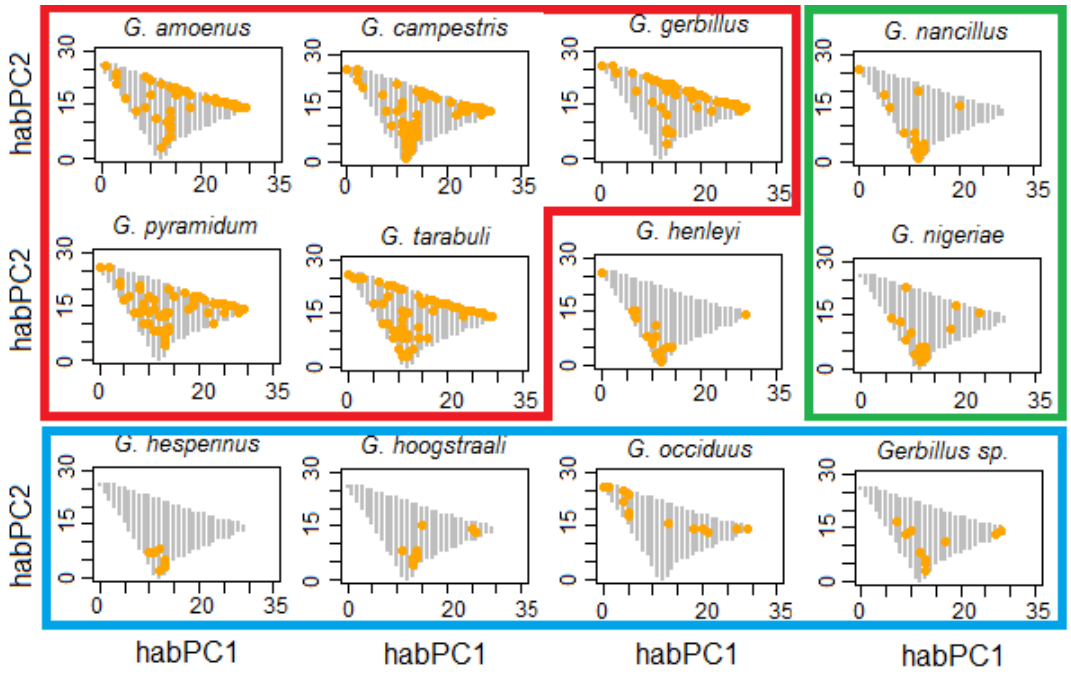

Fig. 7. Distribution of species records (orange points) in relation to the land cover variability of North Africa (grey points). Land cover variability relates to the first two PCAs' axis (habPC1 and habPC2), explaining 83% of variance. Species are grouped per distribution types: wide distribution species (red box), coastal species (blue box) and Sahelian species (green box). *Gerbillus henleyi* does not belong to any group.

4.2 Models of climatic variables

4.2.1 Species distributional drivers

All models resulted with AUCs higher than 0.70 (Table 7). Whilst most models had an AUC of at least 0.80 the models of the coastal species had an AUC of approximately 1.0. Mean diurnal range (Bio2) and Annual Temperature range (Bio7) were generally the most important factors constraining distributions (Table 8); Maximum temperature on the hottest month (Bio5) showed very high importance for the coast species and *G. campestris* while the lowest temperature of the coldest month (Bio7) showed the highest contribution for sahelian species and *G. tarabuli* (Table 8). The precipitation variables were generally less relevant than temperature variables. Mean precipitation on the wettest quarter (Bio16) showed higher contribution values for several wide distribution species, as well as *G. henleyi* and *G. nancillus*, but didn't show relevance for *G. nigeriae* (Table 8). Precipitation on the coldest quarter showed high contribution in species mostly present in the northern areas, as *G. campestris* and *G. hoogstraali*, although the same wasn't found for *G. hesperinus* (Table 8).

Table 7. Models performance metrics. Training and test sample sizes in topo-climatic and landcover models, and corresponding AUC (area under curves) average values (Avg) with standard deviations (SD).

Species	**Samples**		**Training AUC**		**Test AUC**	
	Training	Test	Avg	SD	Avg	SD
G. amoenus	44	11	0.80	0.03	0.77	0.06
G. campestris	90	22	0.85	0.02	0.83	0.05
G. gerbillus	73	18	0.79	0.02	0.78	0.06
G. henleyi	18	1	0.89	0.02	0.92	0.06
G. hesperinus	12	1	0.99	0.00	1.00	0.00
G. hoogstraali	15	1	0.99	0.00	1.00	0.00
G. nancillus	17	1	0.95	0.01	0.94	0.04
G. nigeriae	20	2	0.91	0.02	0.90	0.06
G. occiduus	12	1	0.99	0.00	1.00	0.00
Gerbillus sp.	10	1	0.99	0.00	1.00	0.00
G. pyramidum	56	13	0.73	0.03	0.69	0.06
G. tarabuli	60	15	0.87	0.01	0.86	0.04

Table 8. Average (Avg) contribution values of climatic variables to the respective models of all species and respective standard deviations (SD). Bio2 - Mean diurnal range, Bio5 -Max temperature of warmest month; Bio6 - Min temperature of coldest month, Bio7 - Temperature annual range, Bio16 -Mean precipitation of wettest quarter, Bio19 -Mean precipitation of coldest quarter.

Species	**Bio2**		**Bio5**		**Bio6**		**Bio7**		**Bio16**		**Bio19**	
Gerbillus	Avg	SD	Avg	SD	Avg	SD	Avg	SD	Avg	SD	Avg	SD
amoenus	**59.22**	13.83	2.94	5.50	2.21	2.30	5.03	9.56	**28.67**	8.39	1.76	2.59
campestris	**34.35**	6.03	**21.25**	6.71	2.20	1.33	2.11	3.74	10.29	2.80	**29.80**	7.10
gerbillus	**54.86**	10.83	3.80	3.79	7.10	3.65	12.55	9.09	**20.96**	4.61	0.74	0.86
henleyi	6.51	5.83	0.72	0.87	**41.84**	23.13	**31.89**	20.87	**17.52**	7.79	1.52	0.47
hesperinus	**30.18**	15.43	**61.92**	14.40	0.10	0.11	7.20	2.84	0.12	0.08	0.46	0.26
hoogstraali	5.83	2.49	**68.05**	6.93	2.70	0.94	3.61	2.16	6.02	3.49	**13.79**	2.75
nancillus	16.84	8.61	3.19	3.81	**30.45**	15.57	**18.05**	9.65	**29.42**	8.77	2.05	1.10
nigeriae	2.08	1.75	0.87	1.22	**65.36**	15.81	**20.91**	14.72	5.46	3.61	5.32	1.74
occiduus	**24.74**	4.32	**24.55**	4.46	0.69	0.41	**46.81**	4.10	2.85	0.77	0.35	0.35
sp.	**31.13**	1.71	**36.85**	3.62	2.53	0.72	**18.55**	1.96	2.63	1.20	8.32	1.38
pyramidum	**29.12**	12.87	5.89	4.17	2.11	3.04	7.29	5.56	**54.30**	11.53	1.29	2.03
tarabuli	**17.15**	7.91	0.37	0.52	**23.56**	10.13	**25.88**	10.68	**30.40**	4.26	2.63	1.30

Species responded differently to the climatic variables, e.g. as seen by plotting together their response curves (Fig. 8). All species, except *G. henleyi*, *G. hoogstraali, G. nancillus* and *G. nigeriae*, were limited by high (>10 ºC for coastal species; >16 ºC for other species) mean diurnal temperature ranges (Bio2, Table 8, Fig. 8). Maximum temperature of the hottest month (Bio5) was a limiting factor at high values (>30 ºC) to the coast species and *G. campestris*. Minimum temperature of the coldest month (Bio6) became a limiting factor (<10 ºC) to the Sahelian species and G. *tarabuli* (Fig. 8). The temperature annual range (Bio 7) was limiting at high values to *G. occiduus* and *Gerbillus sp.* (>17,5 ºC, Fig. 8) as well as to the Sahelian species and *G. henleyi* (>22 ºC, Fig. 8). Precipitation of the wettest quarter (Bio16) was the variable that showed highest variance of responses: wide distribution species occurred at low levels of precipitation, while G. *henleyi* and G. *nancillus* occurred in areas of higher precipitation values (150-400 mm, Fig. 8). Precipitation wasn't considered relevant for the distribution of *G. nigeriae*. Precipitation on the coldest quarter (Bio19) was only relevant for *G. campestris* (100-500 mm) and *G. hoogstraali* (80-180mm), which are present in areas of mediterranean influence, but not for *G. hesperinus* (Fig. 8).

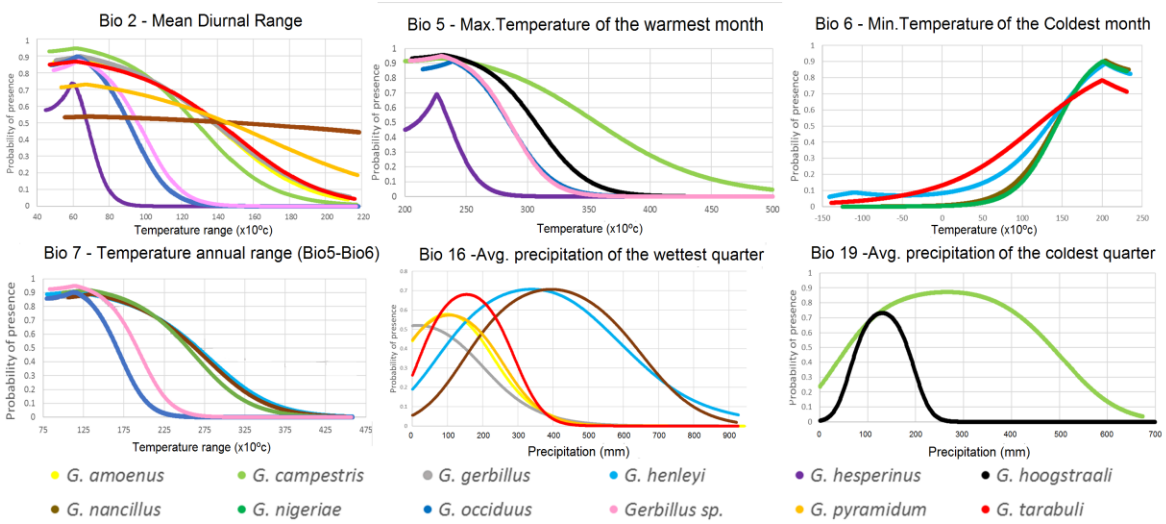

Fig. 8. Response curves of the *Gerbillus* models to climatic variables. All temperatures variables are multiplied by ten to avoid comas.

4.2.2 Climatic models, projections to past conditions, stable climate areas and climatic affinities

Model projections of climate suitability were created for all considered species in the climate conditions of the present day, Middle-Holocene, Last Glacial Maximum and Last Inter-Glacial (Fig. 9-11).

The species with wide distributions (*G. amoenus, G. campestris, G. gerbillus, G. pyramidum, G. tarabuli*) had different projections for the current conditions. The niches of *G. amoenus, G. gerbillus* and *G. pyramidum* had wide niche projections throughout all North Africa. The niche *of G. campestris* was projected specially for the Mediterranean coast of North Africa, as well as in small patches in the Sahel and center of the study area. The niche of *G. tarabuli* was projected more to the south of the Sahara, the Sahel and Atlantic coast, as well as Mediterranean areas in Algeria (Fig. 9). Climate suitability resulted similar to current conditions in the Mid-Holocene for all wide distribution species (Fig. 9). The Last Glacial Maximum had lower climate suitability for all wide distribution species, especially away from the coasts (Fig. 9). The climatic suitability decreased greatly for *G. gerbillus* in the Last Interglacial but was higher for the other wide distribution species (Fig. 9). The climatic stable areas were pointed out on the Atlantic and Mediterranean coast, as well as in areas of known mountain ranges (Fig. 9).

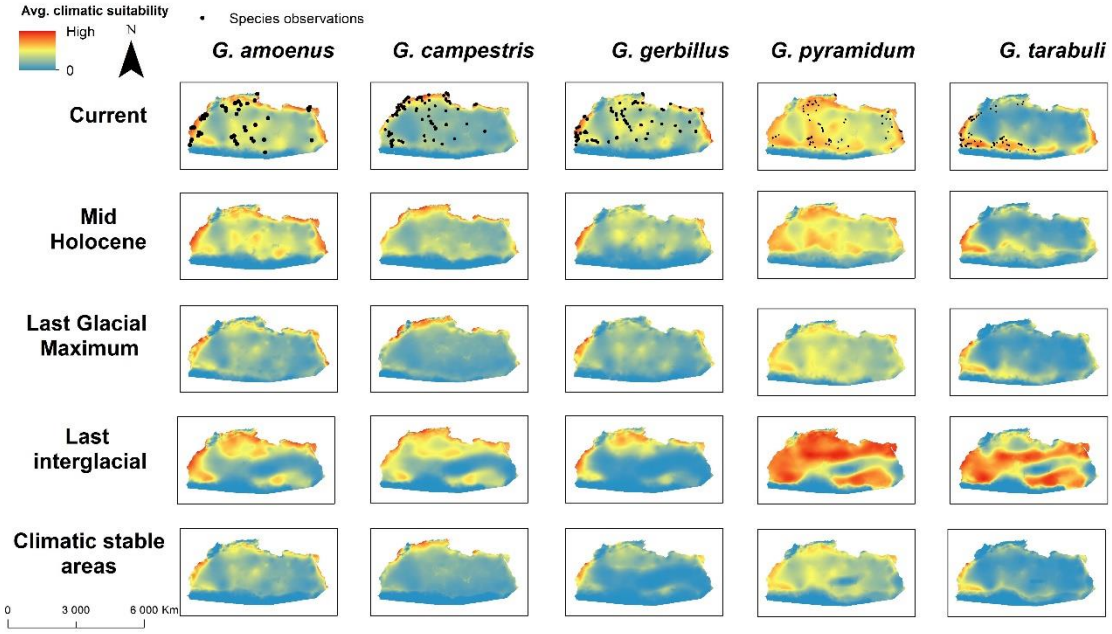

Fig. 9. Models and projections of wide distribution species for the climatic conditions of the present day, Middle Holocene, Last Glacial Maximum and Last Interglacial, as well as corresponding areas of climatic stability. Warmer colors mean higher climate suitability while colder colors mean low climate suitability.

For species with sahelian distributions (*G. nancillus* and *G. nigeriae*) and *G. henleyi*, high climate suitability was indicated throughout all the Sahel even in areas of Eastern Africa where the species are not present. High suitability for *G. henleyi* was also pointed in the Atlantic coast and in some Mediterranean areas of North Africa. Climate suitability in these species was lower than currently during Middle Holocene and Last Glacial Maximum (Fig. 10). The Last Interglacial resulted in larger suitable areas for *G. henleyi* and *G. nancillus*, but only a very restricted area for *G. nigeriae* was detected and only on the Atlantic coast. The stable over time climatic areas were narrow, as the projections for different periods were changing northwards and southwards over geological time (Fig. 10).

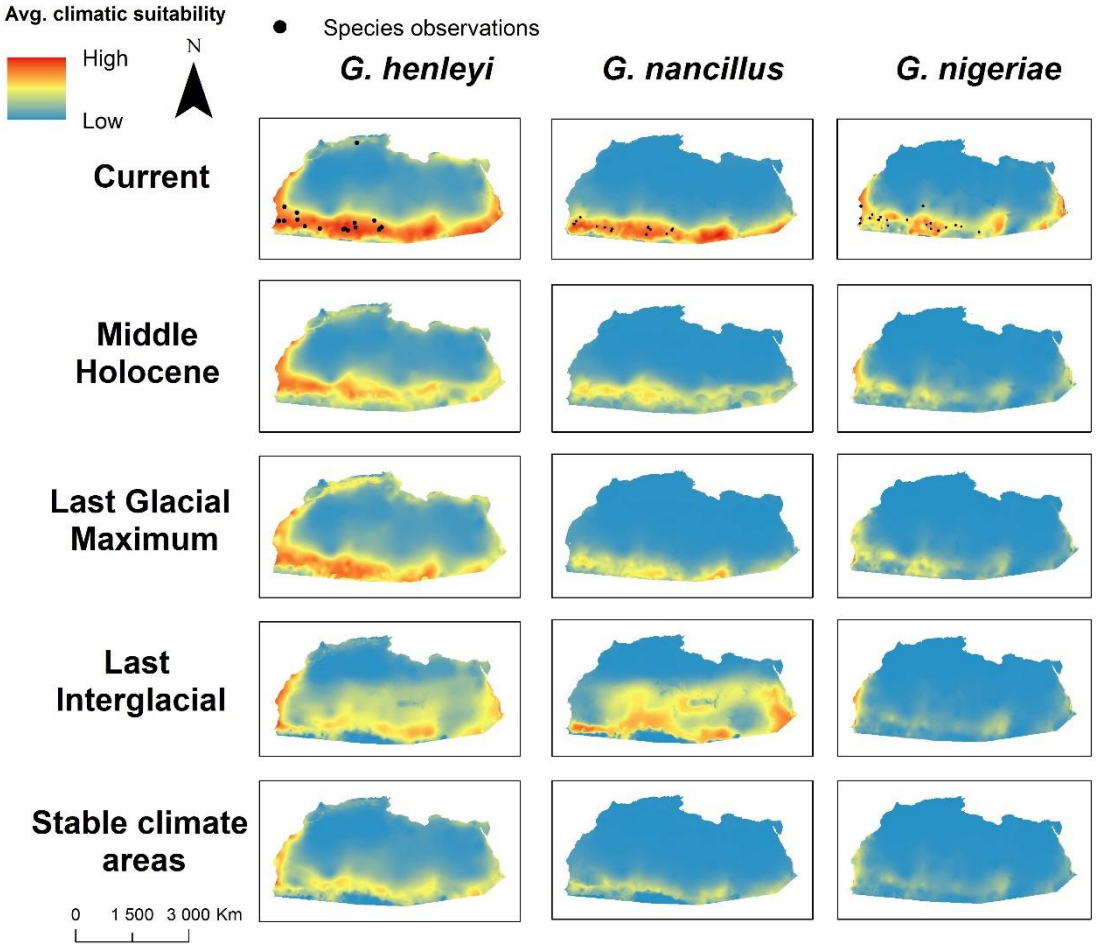

Fig. 10. Models and projections of Sahelian species and *G. henleyi* for the climatic conditions of the present day, Middle Holocene, Last Glacial Maximum and Last Interglacial, as well as corresponding areas of climatic stability. Warmer colors mean higher climate suitability while colder colors mean low climate suitability.

For the species present only on the coast (*G. hesperinus, G. hoogstraali, G. occiduus* and *Gerbillus sp.)* climate suitability areas were similar to the limited areas where they are described to exist today (Fig. 11). The exception was *G. hoogstraali* that was predicted to find suitability in some Mediterranean areas of North Africa, well outside its known distribution. During the Middle Holocene, suitable areas were very similar to current conditions for all coastal species. During the Last Glacial Maximum suitable areas were slightly wider for all coast species, especially for *G. hoogstraali* through the Mediterranean coast of North Africa (Fig. 11). During the Last Interglacial, suitable areas were similar to the present day for *Gerbillus hesperinus*, *G. occiduus* and *Gerbillus. sp.* but smaller for *G. hoogstraali*. The climatic stable areas of the coast species were very limited approximately to the same areas where they are described to exist in the present day (Fig. 11).

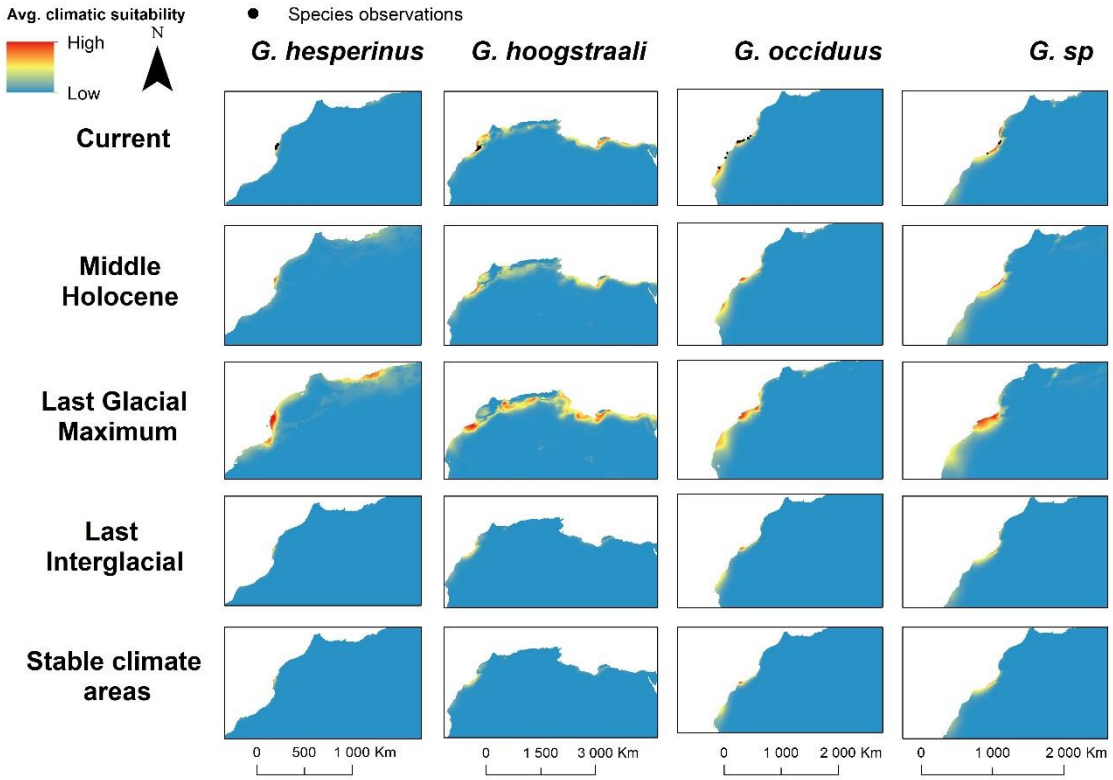

Fig. 11. Models and projections of coast species for the climatic conditions of the present day, Middle Holocene, Last Glacial Maximum and Last Interglacial, as well as corresponding areas of climatic stability. Warmer colors mean higher climate suitability while colder colors mean low climate suitability.

The *Gerbillus* species can be grouped according to ecoregion affinities (Fig. S16-S17). With affinity for Saharan ecoregions are *G. amoenus, G. gerbillus, G. pyramidum.* With an affinity for the sahelian ecoregions are *G. nancillus, G. nigeriae* and *G. henleyi*. With affinity to mediterranean ecoregions are *Gerbillus sp*., *G. hesperinus and G. hoogstraali. Gerbillus campestris* has a mixed affinity for mediterranean and saharan ecoregions and *G. tarabuli* has a mixed affinity for saharan and sahelian ecoregions. At last, *G. occiduus* stands alone as the only species9 with a specific affinity for the Atlantic Sahara (Supplementary material TableS4-S5).

4.3 Topo-climatic and landcover models

4.3.1 Species environmental drivers and reactions to environmental variables

To make it simple to read, topo-climatic and land cover models are hereby called environmental models. These models were performed with the axis tpcPCA and habPCA. The AUC values of all models were higher than 0.7, with values approximate to 1 in the species with limited coastal distribution (Table 9).

The habitat variables affected the models of several species, independently from type of distribution. Of the wide distribution species, *Gerbillus amoenus* and *G. tarabuli* were not affected by any habPC, but rather by tpcPC3 (Table 10). *Gerbillus amoenus* was also affected by tpcPC2 and *G. tarabuli* was also affected tpcPC1 (Table 10). *Gerbillus campestris* and *G. gerbillus* were both affected by the landcover axis that distinguishes bare areas from croplands (habPC3), but *G. campestris was* also affected by tpcPC2 (Table 10). *Gerbillus gerbillus* was not affected by any other variable besides habPC2 and habPC3. The model of G. pyramidum had equal contributions from all variables (Table 10). TpcPC1 was important for both sahelien species, but not for *G. henleyi* (Table 10). *Gerbillus nancillus* and *G. nigeriae* differed in the matter that the former was also considerably affected by tpcPC2 while the latter was more affected by tpcPC3 (Table 10). *Gerbillus henleyi* was only affected by habPC2 and habPC3 (Table 10). All coastal species were affected by tpcPC2 (Table 10). Excepting *G. hoogstraali*, all coastal species were affected by tpcPC1. *Gerbillus hoogstraali* was the only coast species to be considerably affected by a land cover axis (habPC3; Table 10). The least relevant axis for the construction of models was habPC1 (distinguishing sandy bare areas from consolidated bare areas), only being relevant for *G. pyramidum* (Table 10). Because the modeled variables are PCA axis, no response curves were plotted.

Table 9. Training and test sample sizes in topo-climatic and landcover models, and corresponding AUC (area under curves average values (Avg.) with standard deviations (SD).

Species	Samples		Training AUC		Test AUC	
	Training	Test	Avg	SD	Avg	SD
G. amoenus	45	5	0.78	0.03	0.73	0.11
G. campestris	83	20	0.85	0.02	0.81	0.05
G. gerbillus	72	18	0.74	0.03	0.71	0.06
G. henleyi	18	1	0.93	0.02	0.90	0.07
G. hesperinus	12	1	0.99	0.00	1.00	0.00
G. hoogstraali	15	1	0.99	0.00	0.99	0.01
G. nancillus	17	1	0.94	0.01	0.93	0.06
G. nigeriae	20	2	0.93	0.02	0.92	0.05
G. occiduus	12	1	0.99	0.00	1.00	0.00
G. pyramidum	56	13	0.79	0.03	0.77	0.07
Gerbillus sp.	9	1	0.99	0.00	1.00	0.00
G. tarabuli	60	15	0.83	0.03	0.81	0.06

Table 10. Models performance metrics. Average (Avg) contribution of each PCA axis to build the model of each species and respective standard deviations (SD). The suggested interpretation of axis: tpcPC1- Climate seasonality; tpcPC2- Temperature extremes; tpcPC3- Precipitation and altitude; habPC1 - Sandy bare areas to consolidated bare areas; habPC2 - consolidated bare areas to other bare areas; habPC3 - bare areas to croplands and other non-bare areas.

Species	tpcPC1		tpcPC2		tpcPC3		habPC1		habPC2		habPC3	
Gerbillus	Avg	SD	Avg	SD	Avg	SD	Avg	SD	Avg	SD	Avg	SD
amoenus	3.19	3.20	**33.41**	12.06	**27.34**	9.95	13.80	10.05	9.26	7.61	12.99	8.09
campestris	3.47	3.09	**58.69**	6.14	6.17	2.48	5.60	2.98	7.45	2.74	**18.62**	4.46
gerbillus	4.53	3.65	4.89	4.06	4.34	4.30	3.74	3.00	**33.39**	8.43	**46.49**	8.48
henleyi	11.42	12.55	10.09	7.79	12.67	5.96	1.69	2.06	**29.73**	11.19	**34.40**	14.30
hesperinus	**21.29**	2.74	**71.53**	3.51	3.45	1.60	0.49	0.34	0.62	0.75	2.62	1.38
hoogstraali	8.63	4.04	**61.29**	5.58	9.37	2.32	0.01	0.02	2.35	2.37	**18.35**	4.05
nancillus	**22.74**	13.16	**22.71**	5.31	3.68	4.55	0.40	0.62	**26.73**	7.41	**23.74**	9.61
nigeriae	**38.81**	19.95	4.86	3.99	**19.05**	6.91	1.32	1.76	**16.32**	7.95	**19.64**	10.85
occiduus	**26.97**	2.91	**41.10**	3.07	**29.62**	5.64	0.59	0.59	0.70	0.74	1.02	1.16
pyramidum	**15.00**	5.13	10.96	5.82	**22.47**	7.53	**18.18**	11.08	**14.69**	7.61	**18.70**	7.24
sp.	**36.22**	3.02	**47.14**	1.26	13.13	1.60	0.06	0.13	0.44	1.11	3.01	1.59
tarabuli	**24.03**	9.01	5.27	3.19	**50.25**	9.29	5.67	3.83	8.77	8.06	6.01	3.16

4.3.2 Models of environmental suitability and species richness patterns

The models constructed with climatic and habitat variables were similar to models constructed with climatic variables only, but with less continuous gradients between suitable and non-suitable areas (Fig. 12). Especially the model of environmental suitability of *G. campestris* (Fig. 12) revealed more fragmented distribution of suitability than the map of climate suitability (Fig. 9).

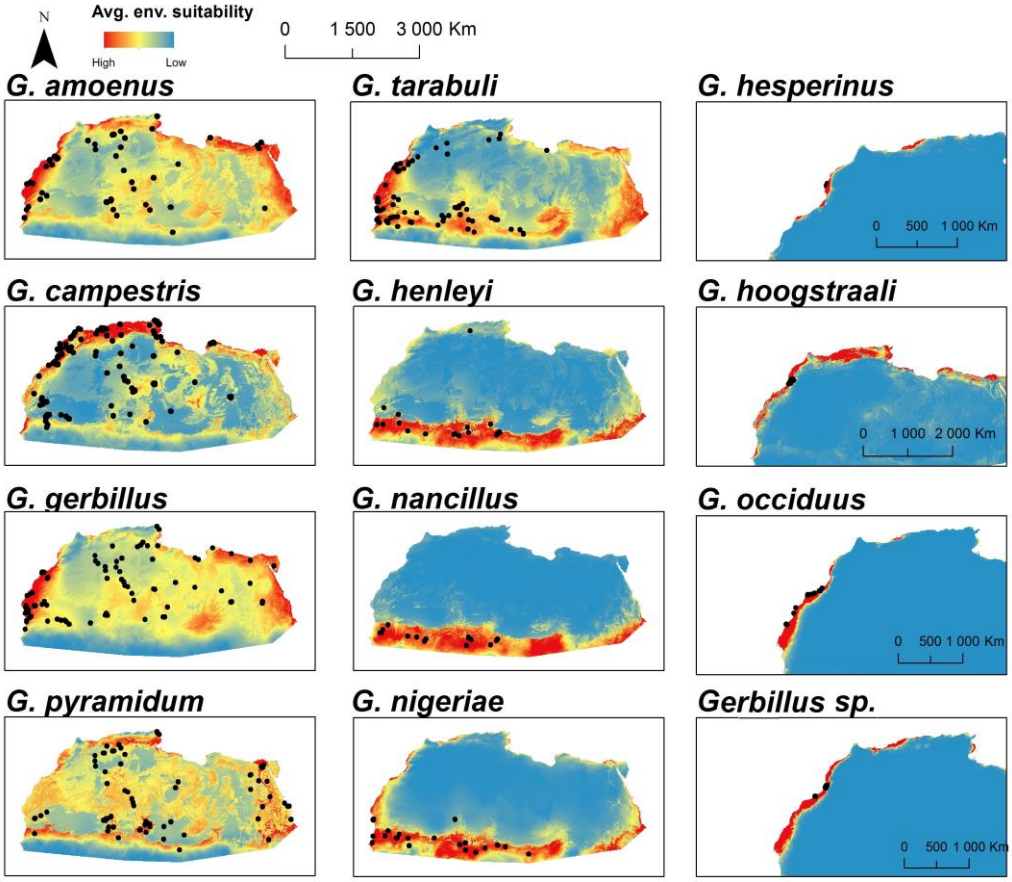

Fig. 12. Models derived from current topo-climatic and land cover variables. Warmer colors mean higher environmental suitability and colder colors mean lower environmental suitability. Projections of the coast species have been zoomed independently and have corresponding scales on the right side.

The representation of potential species richness highlights many parts of the Atlantic coast, and parts of the Sahel, as major potential species rich areas (Fig. 13). The areas with lower species richness are away from the coast, especially in the area corresponding to the upper Atlas mountains and the areas corresponding to inland Mauritania, Mali and Algeria (Fig. 13). A second representation of species richness was generated excluding *Gerbillus sp.* (Supplementary material Fig. S26)

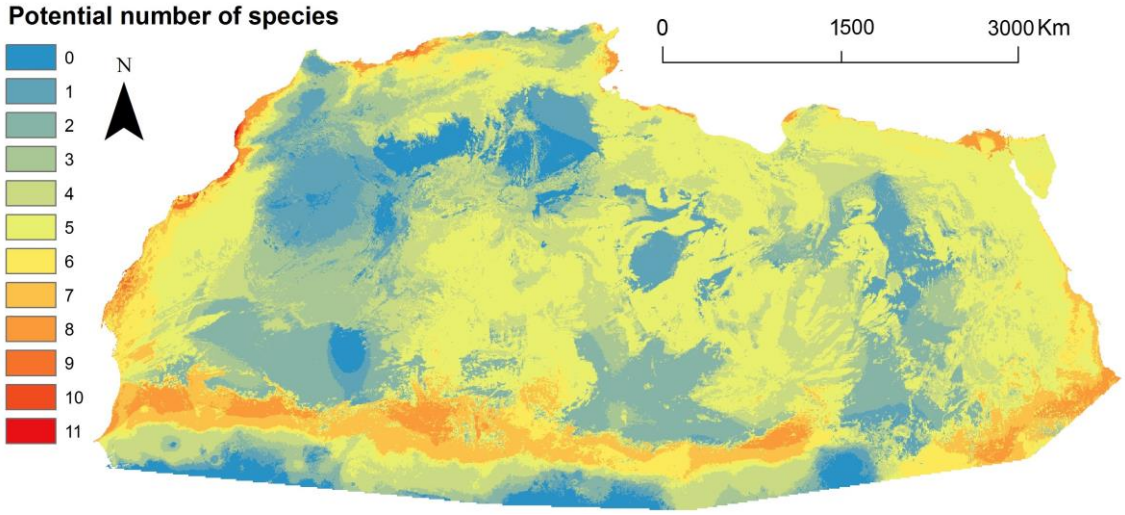

Fig. 13. Potential species richness, based on the ecological models of every considered species. Warmer colors show areas with environmental suitability for most species at the same time (Maximum 11) and colder colors show areas with environmental suitability for the least species (Minimum 0).

4.4 Overlap of ecological niches

When considering climatic data, the overlap of the modeled ecological niches varied from 0.04 to 0.91 (Schoener's D; Table 11). The wide distribution species had high levels of niche overlap (>0.70; Table 11), especially *G. amoenus* with G. gerbillus and with *G. pyramidum* (0.91; Table 11) and *G. pyramidum* with *G. gerbillus* (0.88; Table 11). The sahelian species had high niche overlap (0.78; Table 11). The coast species had low niche overlap (<0.30; Table 11) apart from *G. occiduus* and *Gerbillus sp.* that had a moderate level of niche overlap (0.53; Table 11). Gerbillus *henleyi* had high niche overlap with the sahelian species (>0.75; Table 11) and with *G. tarabuli* (0.73; Table 11). The overlap between coastal species and the others was always low (<0.30; Table 11). The overlap between wide distribution species and sahelian species was low (<50; Table 11) apart from *G. tarabuli* which presented an intermediate overlap with *G. nancillus* (0.51; Table 11) and *G. nigeriae* (0.64; Table 11).

Most climatic identity tests reject niche equivalency for species comparisons (Table 11; Supplementary material Fig. S29-S32). However, most climatic background tests show that species select background data in a similar way, since the distribution of background tests is lower than the actual niche overlap between species (Table 11; Supplementary material Fig. S33-S42). The climatic background of the niche of *G. hoogstraali* shows differentiation against the observation points of *G. campestris*, *G. henleyi* and *G. nigeriae*. However, the climatic background of the latter species doesn't show differentiation against the observation points of *G. hoogstraali* (Table 11;

Supplementary material Fig. S33-S42). No hypothesis tests are presented for *Gerbillus sp*, since they had unclear distributions.

Table 11. Results of D overlap (Schoener, 1968), niche identity and background tests for all species comparisons when using climatic models. Significant results (<0.05) are outlined in bold; *: Background tests that indicate that niches are not similar.

Climatic data					
		Schoener's D	Identity test	Background tests	
				Sp1vsSp2	Sp2vsSp1
Sp1	Sp2		(p value)	(p value)	(p value)
G. campestris	*G. amoenus*	0.86	0.435	**0.039**	**0.039**
G. gerbillus	*G. amoenus*	0.91	**0.043**	**0.039**	**0.039**
G. henleyi	*G. amoenus*	0.55	**0.043**	**0.039**	**0.039**
G. hesperinus	*G. amoenus*	0.08	**0.043**	**0.039**	**0.039**
G. hoogstraali	*G. amoenus*	0.21	**0.043**	**0.039**	0.118
G. nancillus	*G. amoenus*	0.33	**0.043**	**0.039**	**0.039**
G. nigeriae	*G. amoenus*	0.43	**0.043**	**0.039**	0.667
G. occiduus	*G. amoenus*	0.16	**0.043**	**0.039**	**0.039**
G. pyramidum	*G. amoenus*	0.91	**0.049**	**0.039**	**0.039**
Gerbillus sp.	*G. amoenus*	0.17	**-**	**-**	**-**
G. tarabuli	*G. amoenus*	0.73	**0.043**	**0.039**	0.627
G. gerbillus	*G. campestris*	0.79	**0.043**	**0.039**	**0.039**
G. henleyi	*G. campestris*	0.53	**0.043**	0.078	**0.039**
G. hesperinus	*G. campestris*	0.11	**0.043**	**0.039**	**0.039**
G. hoogstraali	***G. campestris***	0.28	**0.043**	**0.039**	**0.039***
G. nancillus	*G. campestris*	0.33	**0.043**	**0.039**	**0.039**
G. nigeriae	*G. campestris*	0.40	**0.043**	0.627	0.706
G. occiduus	*G. campestris*	0.17	**0.043**	**0.039**	**0.039**
G. pyramidum	*G. campestris*	0.83	0.261	**0.039**	**0.039**
Gerbillus sp.	*G. campestris*	0.20	**-**	**-**	**-**
G. tarabuli	*G. campestris*	0.69	**0.043**	0.235	0.078
G. henleyi	*G. gerbillus*	0.51	**0.043**	**0.039**	**0.039**
G. hesperinus	*G. gerbillus*	0.07	**0.043**	**0.039**	**0.039**
G. hoogstraali	*G. gerbillus*	0.18	**0.043**	0.196	0.078
G. nancillus	*G. gerbillus*	0.29	**0.043**	**0.039**	**0.039**
G. nigeriae	*G. gerbillus*	0.40	**0.043**	**0.039**	0.314
G. occiduus	*G. gerbillus*	0.17	**0.043**	**0.039**	**0.039**
G. pyramidum	*G. gerbillus*	0.88	0.565	**0.039**	**0.039**
Gerbillus sp.	*G. gerbillus*	0.17	**-**	**-**	-
G. tarabuli	*G. gerbillus*	0.69	**0.043**	0.235	**0.039**
G. hesperinus	*G. henleyi*	0.06	**0.043**	0.118	**0.039**
G. hoogstraali	***G. henleyi***	0.13	**0.043**	0.549	**0.039***
G. nancillus	*G. henleyi*	0.75	0.696	**0.039**	**0.039**
G. nigeriae	*G. henleyi*	0.81	0.391	**0.039**	0.078
G. occiduus	*G. henleyi*	0.14	**0.043**	**0.039**	**0.039**

Climatic data					
		Schoener's D	Identity test	Background tests	
				Sp1vsSp2	Sp2vsSp1
Sp1	Sp2		(p value)	(p value)	(p value)
G. pyramidum	*G. henleyi*	0.56	**0.043**	**0.039**	**0.039**
Gerbillus sp.	*G. henleyi*	0.13	**-**	**-**	**-**
G. tarabuli	*G. henleyi*	0.73	0.130	**0.039**	**0.039**
G. hoogstraali	*G. hesperinus*	0.25	**0.043**	**0.039**	**0.039**
G. nancillus	*G. hesperinus*	0.02	**0.043**	**0.039**	**0.039**
G. nigeriae	*G. hesperinus*	0.03	**0.043**	0.235	0.275
G. occiduus	*G. hesperinus*	0.24	**0.043**	**0.039**	0.118
G. pyramidum	*G. hesperinus*	0.06	**0.043**	**0.039**	**0.039**
Gerbillus sp.	*G. hesperinus*	0.32	**-**	**-**	**-**
G. tarabuli	*G. hesperinus*	0.06	**0.043**	**0.039**	**0.039**
G. nancillus	*G. hoogstraali*	0.04	**0.043**	0.627	**0.039**
G. nigeriae	***G. hoogstraali***	0.06	**0.043**	**0.039***	0.118
G. occiduus	*G. hoogstraali*	0.24	**0.043**	0.157	**0.039**
G. pyramidum	*G. hoogstraali*	0.17	**0.043**	0.078	0.627
Gerbillus sp.	*G. hoogstraali*	0.51	**-**	**-**	**-**
G. tarabuli	*G. hoogstraali*	0.18	**0.043**	0.157	0.118
G. nigeriae	*G. nancillus*	0.78	0.913	**0.039**	**0.039**
G. occiduus	*G. nancillus*	0.07	**0.043**	**0.039**	**0.039**
G. pyramidum	*G. nancillus*	0.36	**0.043**	**0.039**	**0.039**
Gerbillus sp.	*G. nancillus*	0.05	**-**	**-**	**-**
G. tarabuli	*G. nancillus*	0.51	**0.043**	**0.039**	**0.039**
G. occiduus	*G. nigeriae*	0.14	**0.043**	0.353	0.471
G. pyramidum	*G. nigeriae*	0.43	**0.043**	0.118	**0.039**
Gerbillus sp.	*G. nigeriae*	0.09	**-**	-	-
G. tarabuli	*G. nigeriae*	0.64	**0.043**	**0.039**	**0.039**
G. pyramidum	*G. occiduus*	0.12	**0.043**	**0.039**	**0.039**
Gerbillus sp.	*G. occiduus*	0.53	**-**	**-**	**-**
G. tarabuli	*G. occiduus*	0.18	**0.043**	**0.039**	**0.039**
Gerbillus sp.	*G. pyramidum*	0.13	**-**	**-**	**-**
G. tarabuli	*G. pyramidum*	0.72	**0.043**	0.118	0.784
G. tarabuli	*Gerbillus sp.*	0.17	**-**	**-**	**-**

When considering topo-climatic and land cover data, the measures of ecological niche overlap vary between 0.02 and 0.87 (Schoener's D; Table 12). The patterns of niche overlap are the same as with climatic data. Wide distribution species have high overlap (>0.67; Table 12). Sahelian species have high overlap (0.76; Table 12). Coastal species have low overlap (<0.38; Table 12) except for *G. occiduus* and *Gerbillus sp.* (0.67; Table 12).

The comparison between *G. amoenus* and *G. tarabuli* is inconclusive and no niche differentiation could be found, even though they have such a high overlap (0.77; Table 12). Whenever the tests were significant, niche equivalency was rejected but the background data was always more similar than expected (Table 12). In contrast with the climatic data there was no differentiation of niches between *G. hoogstraali* and *G. campestris* or *G. henleyi* and *G. nigeriae.* There was no single case of niche differentiation in these results.

Table 12. Results of D overlap (Schoener, 1968), niche identity and background tests for all species comparisons when using topo-climatic and landcover models. Significant results (<0.05) are outlined in bold.

Topo-climatic and land cover data					
		Schoener's D	Identity test	Background tests	
				Sp1vsSp2	Sp2vsSp1
Sp1	Sp2		(p value)	(p value)	(p value)
G. campestris	*G. amoenus*	0.79	0.824	**0.039**	0.78
G. gerbillus	*G. amoenus*	0.87	0.353	**0.039**	**0.039**
G. henleyi	*G. amoenus*	0.48	**0.039**	0.549	**0.039**
G. hesperinus	*G. amoenus*	0.06	**0.039**	**0.039**	**0.039**
G. hoogstraali	*G. amoenus*	0.39	**0.039**	**0.039**	0.078
G. nancillus	*G. amoenus*	0.31	**0.039**	**0.039**	**0.039**
G. nigeriae	*G. amoenus*	0.47	**0.039**	**0.039**	**0.039**
G. occiduus	*G. amoenus*	0.12	**0.039**	**0.039**	0.431
G. pyramidum	*G. amoenus*	0.87	0.157	**0.039**	**0.039**
Gerbillus sp.	*G. amoenus*	0.13	**-**	-	-
G. tarabuli	*G. amoenus*	0.77	0.235	0.078	0.078
G. gerbillus	*G. campestris*	0.68	**0.039**	0.667	**0.039**
G. henleyi	*G. campestris*	0.49	**0.039**	0.902	0.078
G. hesperinus	*G. campestris*	0.09	**0.039**	**0.039**	**0.039**
G. hoogstraali	*G. campestris*	0.48	**0.039**	**0.039**	0.078
G. nancillus	*G. campestris*	0.32	**0.039**	**0.039**	**0.039**
G. nigeriae	*G. campestris*	0.46	**0.039**	0.078	0.118
G. occiduus	*G. campestris*	0.12	**0.039**	**0.039**	0.118
G. pyramidum	*G. campestris*	0.77	0.118	0.471	**0.039**
Gerbillus sp.	*G. campestris*	0.16	**-**	**-**	-
G. tarabuli	*G. campestris*	0.67	**0.039**	0.549	0.118
G. henleyi	*G. gerbillus*	0.39	**0.039**	**0.039**	0.078
G. hesperinus	*G. gerbillus*	0.04	**0.039**	**0.039**	**0.039**
G. hoogstraali	*G. gerbillus*	0.35	**0.039**	**0.039**	0.078
G. nancillus	*G. gerbillus*	0.24	**0.039**	**0.039**	**0.039**
G. nigeriae	*G. gerbillus*	0.42	**0.039**	**0.039**	0.118
G. occiduus	*G. gerbillus*	0.12	**0.039**	**0.039**	0.196
G. pyramidum	*G. gerbillus*	0.81	0.118	**0.039**	0.471

Topo-climatic and Land cover data					
		Schoener's D	Identity test	Background tests	
				Sp1vsSp2	Sp2vsSp1
Sp1	Sp2		(p value)	(p value)	(p value)
Gerbillus sp.	*G. gerbillus*	0.13	-	**-**	-
G. tarabuli	*G. gerbillus*	0.76	**0.039**	**0.039**	0.941
G. hesperinus	*G. henleyi*	0.04	**0.039**	0.824	**0.039**
G. hoogstraali	*G. henleyi*	0.23	**0.039**	**0.039**	0.471
G. nancillus	*G. henleyi*	0.79	0.275	**0.039**	**0.039**
G. nigeriae	*G. henleyi*	0.86	**0.039**	**0.039**	**0.039**
G. occiduus	*G. henleyi*	0.10	**0.039**	0.235	0.118
G. pyramidum	*G. henleyi*	0.47	**0.039**	**0.039**	**0.039**
Gerbillus sp.	*G. henleyi*	0.10	**-**	-	-
G. tarabuli	*G. henleyi*	0.56	**0.039**	0.078	**0.039**
G. hoogstraali	*G. hesperinus*	0.22	**0.039**	**0.039**	**0.039**
G. nancillus	*G. hesperinus*	0.02	**0.039**	**0.039**	**0.039**
G. nigeriae	*G. hesperinus*	0.06	**0.039**	**0.039**	1.000
G. occiduus	*G. hesperinus*	0.19	**0.039**	**0.039**	0.512
G. pyramidum	*G. hesperinus*	0.04	**0.039**	**0.039**	**0.039**
Gerbillus sp.	*G. hesperinus*	0.33	**-**	**-**	**-**
G. tarabuli	*G. hesperinus*	0.04	**0.039**	**0.039**	**0.039**
G. nancillus	*G. hoogstraali*	0.12	**0.039**	0.078	**0.039**
G. nigeriae	*G. hoogstraali*	0.25	**0.039**	0.118	**0.039**
G. occiduus	*G. hoogstraali*	0.24	**0.039**	0.157	**0.039**
G. pyramidum	*G. hoogstraali*	0.36	**0.039**	0.078	**0.039**
Gerbillus sp.	*G. hoogstraali*	0.38	**-**	-	**-**
G. tarabuli	*G. hoogstraali*	0.33	**0.039**	0.078	**0.039**
G. nigeriae	*G. nancillus*	0.76	0.941	**0.039**	**0.039**
G. occiduus	*G. nancillus*	0.06	**0.039**	**0.039**	**0.039**
G. pyramidum	*G. nancillus*	0.31	**0.039**	**0.039**	**0.039**
Gerbillus sp.	*G. nancillus*	0.05	**0.039**	**0.039**	**0.039**
G. tarabuli	*G. nancillus*	0.42	**0.039**	**0.039**	**0.039**
G. occiduus	*G. nigeriae*	0.14	**0.039**	0.275	0.392
G. pyramidum	*G. nigeriae*	0.44	**0.039**	**0.039**	**0.039**
Gerbillus sp.	*G. nigeriae*	0.14	**-**	-	-
G. tarabuli	*G. nigeriae*	0.60	**0.039**	0.235	**0.039**
G. pyramidum	*G. occiduus*	0.09	**0.039**	0.078	**0.039**
Gerbillus sp.	*G. occiduus*	0.67	**0.039**	**0.039**	**0.039**
G. tarabuli	*G. occiduus*	0.14	**0.039**	0.196	**0.039**
Gerbillus sp.	*G. pyramidum.*	0.10	**-**	**-**	-
G. tarabuli	*G. pyramidum*	0.73	**0.039**	**0.039**	0.275
G. tarabuli	*Gerbillus sp.*	0.13	**0.039**	**0.039**	0.078

5 Discussion

5.1 Species distribution updates and predicted suitability areas

Most models created for the considered species overlap the corresponding distributions described in IUCN. Furthermore, the IUCN distribution maps of some species (*G. amoenus, G. campestris*, *G. nigeriae*, G*. occiduus* and *G. pyramidum*) are incomplete and should be expanded with the new samples included in this study (Supplementary material Fig. S1).

The first hypothesis was that the studied species are constrained by topo-climatical and landcover factors, and not just by historical factors and population dynamics (Hubbell 2001). This hypothesis was corroborated by most models, which projected environmental suitability to the areas occupied by the species, with suitability declines in areas of sharp environmental gradients that coincide with the species range limits (Fig. 9-11). The exceptions were *G. hoogstraali, G. nigeriae* and *G. pyramidum* for which the estimated areas of occurrence (Fig. 9-11) were considerably greater than the described distribution ranges (Aulagnier & Hutterer 2008; Granjon 2016c). Likewise, the predicted areas of occurrence for those three species and the new undescribed species (*Gerbillus sp.)* extended beyond available samples. This might be explained by physical and biological barriers that were not considered by models. The Atlas mountain range is the most probable barrier to an eastern dispersal of *G. hoogstraali* (Lay 1983). *Gerbillus nigeriae* had high predicted suitability along Atlantic coast, from Senegal to north Morocco (Fig. 11) but no single observation is available north of Mauritania (Supplementary material Fig. S1). Perhaps it is outcompeted in the north by the coastal species, the same way it faces competition in the south with tropical species (Thiam et al. 2008; 2011). *Gerbillus sp.* was also predicted to find suitability along the all Atlantic coast of Morocco, but only a few samples were found in the central coast (Supplementary material Fig. S1; Table S2). It is possible that the species exists in other areas and hasn't yet been molecularly identified, more fieldwork and molecular barcoding are suggested to clear this doubt. *Gerbillus pyramidum* is predicted to have a very wide distribution, different from the one described in IUCN (Aulagnier & Granjon 2016). Despite being mostly concordant with the distribution of samples, *G. pyramidum* is predicted here to exist in Morocco (Fig. 9), where no specimens have been found so far (Supplementary material Fig. S1). Again, the Atlas mountains seem to represent a barrier of dispersal to northern Morocco, but no obvious barrier exists on south Morocco. The area between central Algeria and south Morocco is unsampled (Fig. 3; Supplementary material Fig. 14)

and corresponds to an area of extreme climate (Schulz et al. 2009) and insecurity for fieldwork (Brito et al. 2014). Specimens of *G. pyramidum* have been found in Mauritania but perhaps these populations have no connectivity to the rest of the species.

The species were grouped according to distribution types: Wide, Coastal or Sahelian distribution. When overlapping the species models with ecoregions, it is possible to see different affinities (Tables 16-17). The wide distribution species are predicted to exist in all considered ecoregions. The Sahelian species are predicted to exist to Sahelian ecoregions. The coastal species, except for *G. occiduus*, are predicted to exist mainly in mediterranean ecoregions Tables (16-17). In this sense, *G. occiduus* is unique since it is mainly predicted to exist in the small Atlantic Sahara ecoregion and not in the others. Perhaps this is the species most adapted to ecosystems dependent on fog humidity coming from the ocean (Shanyengana et al. 2002).

5.2 Species distributional drivers

The wide distribution species (*G. amoenus, G. campestris, G. gerbillus, G. pyramidum* and *G. tarabuli*) had diverse patterns. *Gerbillus campestris* presence appears to be related with cropland areas (Table 10). Oppositely, *G. gerbillus* appears to avoid croplands, inhabiting mainly bare areas (Table 10). The probability of presence of *G. gerbillus* peaked close to 0 mm of precipitation (Fig. 8), which highlights its true affiliations with extremely dry regions, possibly outcompeted in areas of higher precipitation and resources. The affinity of *G. gerbillus* for extreme conditions had already been pointed by physiological studies (Burns & Balekjian 1956; Khalil & Tawfic 1963) but it is the first time showed here using Ecological Niche Modeling. It is also the first time that environmental reactions are compared between several species of *Gerbillus*. *Gerbillus pyramidum* and *G. amoenus* seem to follow *G. gerbillus* ecological patterns (Fig. 8), but are more sensible to extreme temperature ranges. *Gerbillus tarabuli* appears to be absent from the most continental areas of North Africa where it was thought to exist (Supplementary material Fig. S1), and exist more in western Sahel and western periphery of Sahara (Fig. 9). As for the sahelian species (*G. nancillus* and *G. nigeriae*), both select areas with higher minimum temperatures, but only *G. nancillus* is affected by precipitation variables (Table 8). This means that, while both species occupy the Sahel, *Gerbillus nancillus* tends to occupy areas with more tropical influence, with lower annual temperature extremes and higher precipitation, while *G. nigeriae* just avoids areas with low minimum temperatures (Fig. 8), and can also persist northwards along the Atlantic coast where these temperatures don't drop so much in winter. The coastal species (*G. hesperinus, G. hoogstraali, G. occiduus* and *Gerbillus sp.*) appear to be strongly

constrained by climate (Table 8), especially by large temperature ranges and high maximum temperatures (Fig. 8). The predicted areas of occurrence of these species were restricted like their actual distributions, which suggests they only thrive in very specific climates, and fail to expand either due to competition and/or to physiological stress. Perhaps, in the possibility of having speciated in isolation due to shifting sea level (Weisrock 2012), these species lost mechanisms to cope with heat stress and extreme aridity as effectively as their wide distribution counterparts. Precipitation was not considered relevant for the coastal species (Table 8) but it is important to note that the coastal areas have a second source of humidity, fog arriving from ocean (Żmudzka et al. 2014), that was not available as a modelling variable. Even though fog is considered to not have an effect in the deep soil moisture (Żmudzka et al. 2014) it is instrumental for the existence of moss, lichens and succulent plants (Rundel 1978; Shmida 1985). There are no studies on the possible influence of fog in the distribution of animals in North Africa (Koračin et al. 2014). In contrast, the fogs of the Namib desert in South Africa have been mapped (Olivier 1995), studied for their influence in ecosystems (Shanyengana et al. 2002), including in grasses (Roth-Nebelsick et al. 2012) and beetles (Nørgaard & Dacke 2010). Ideally, fog humidity and its influence in primary productivity should be measured on the coasts of North Africa. These measurements should then be included in modeling approaches of coast species like the ones used in this study. In this study, fog humidity might be indirectly represented by the maximum temperature in the hottest month, explaining why it was so relevant for the coastal species.

In summary, the studied Gerbillus species that inhabit Northwestern Africa seem to be mainly constrained by temperature ranges (Table 8). Apart from *G. campestris, G. henleyi* and *G. nancillus*, the studied *Gerbillus* go against the general rule that endotherms are mainly dependent on primary productivity (Buckley et al. 2012). In this aspect, they might be more similar with ectotherms, a result of adaptation to extremely dry conditions and low availability of resources. Their distributions seem to be more limited by cold than by hot temperatures, which makes sense when considering that these animals are nocturnal and spend the hot daytime inside their burrows (Torre et al. 2007). The energetic cost of maintaining body temperatures in cold periods can be quite high (Glanville & Seebacher 2010), and eventually there is a threshold when most species can't survive and thrive in areas of poor resources. Moreover, the correctness of the used temperature variables for modeling distributions of burrow-living animals should be discussed. While it appears that minimum temperatures impact directly the activity of gerbils (Bakken 1992), there is little work on the relation between air temperature and the temperature that the animals experience, their operative

temperature (Alagaili et al. 2017). The operative temperature of animals is influenced by factors as wind, humidity, contact with ground or sheltering (Bakken 1992). Gerbils maximum operative temperature must be different from maximum air temperature, given they shelter in burrows during the daytime. This is why most species were not affected by maximum temperatures. However, the results indicate that maximum temperatures might still impact sheltered animals, since the coastal species and *G. campestris* avoided high maximum temperatures (Table 8). How are they affected by maximum temperatures? Perhaps they make shallow burrows? The case of *G. campestris* comes in agreement with literature, which describes shallow burrows for the species (Petter 1961 in Granjon & Duplantier 2009). In the case of the coastal species it could also be an indirect effect, since maximum temperatures seem to be low close to the ocean, where there is fog humidity. To resolve this question, maximum operative temperature (Bakken 1992) should be considered instead of maximum air temperature. It might be interesting to compare operative temperature of *G. campestris* and coastal species with the operative temperature of any other studied *Gerbillus*, as done for other species of rodents (Alagaili et al. 2017). This is more relating to mechanistic modeling (Kearney & Porter 2009) and requires a bigger experimental effort to perform, something that correlative modeling does not. Perhaps by using hybrid modeling approaches (considering a mixture of spatial and demographic variables that need being previously studied) can one get optimized results (Fordham et al. 2013; Fordham et al. 2014).

5.3 Projections to past climates and climatically stable areas

The hypothesis that the humid periods would decrease distributions for widely distributed desert *Gerbillus* species and increase distributions for Coastal and Sahelian *Gerbillus* species did not prove true with the obtained results. The suitability projections in the humid Middle Holocene (MH) were similar to the present-day projections in all widely distributed and coastal species (Fig. 9 and 11). For the Sahelian species and *G. henleyi*, the projections of MH were even smaller than in current conditions (Fig. 10), oppositely to expected. These results can be due to the very high importance of temperature variables for the predicting distributions of all *Gerbillus* species, which didn't change much between the current period and MH (Gent et al. 2011; Watanabe et al. 2011). The fact that the coast species might be dependent on fog humidity hinders their projections to the past. If their relation with primary productivity cannot be assumed with current precipitation patterns, projecting models to higher precipitation patterns does not show higher climatic suitability. Only after understanding the relation between fog

humidity and primary precipitation in the area, can these species distributions be projected to the past with confidence.

The less cold and less dry conditions of the Last Interglacial (LIG) were the most favorable for many species of wide distribution: *G. campestris*, *G. pyramidum* and *G. tarabuli*. The Last Interglacial had generally smaller diurnal temperature ranges in North Africa (Gent et al. 2011; Watanabe et al. 2011). The projections of these species in LIG show higher suitabilities in northwestern Africa, where precipitation levels were slightly higher than nowadays (Gent et al. 2011; Watanabe et al. 2011). Studies claim that during the Last Interglacial, the African monsoon shifted up to 1,000 km north of its location today, especially in eastern Africa, in modern day Chad and Egypt (Rohling et al. 2002; Coulthard et al. 2013). These areas correspond to low suitabilities for all widely distributed species (Fig. 9). In contrast, *G. nancillus* and *G. henleyi* were projected to find higher suitability in those same areas of higher precipitation (Fig. 9). *Gerbillus nancillus* and *G. henleyi* were the species that mostly selected high precipitations (Fig. 8), therefore their distributions must have followed the precipitation shifts.

The Last Glacial Maximum (LGM) appears to have had the smallest climatic suitabilities for all species (Fig. 9-10), except for the coastal species (Fig. 11). The coastal species had expanded areas of climatic suitability in LGM, perhaps because the extended stretches of land (with a lower sea level) had a strong climatic influence from the Atlantic, with low maximum temperatures (Gent et al. 2011; Watanabe et al. 2011) or fog humidity. The conclusion relating to this hypothesis is that the shifting precipitation patterns only changed species distributions when accompanied by changes in temperature ranges, which are the main constraint for all species. The importance of Atlantic coast of North Africa is highlighted by the maps of climate stability (Fig. 9-11), which show higher continuous suitabilities on the coast for most species. This makes sense when considering that the Atlantic influence has been a permanent influence on temperature ranges, not allowing them to be too extreme (Le Houerou 1997). The only species for which the Atlantic coast was less relevant as a climatically stable area was *G. nancillus*, since it depends more on the monsoon precipitation patterns than temperature variables (Table 8). It is also the species with smallest stable suitability areas (Fig. 11), derived from the latitudinal shifts of the precipitation patterns. This pattern has already been verified in other mammals (Martínez-Meyer et al. 2004) as a result of niche conservatism (Peterson et al. 1999).

5.4 Spatial richness patterns and species coexistence

The hypothesis that higher species richness should be found in areas of milder climates and intermediate precipitation (as a proxy for primary productivity) is addressed by the overlapped models of suitability for all species (Fig. 13). Since there are other unconsidered species of *Gerbillus* in Northern Africa, only its western coast will be considered for discussion. In the map produced by this thesis, the areas with highest potential species richness seem to coincide roughly with the Atlantic coast and Sahelian belt (Fig. 13). Very importantly, these areas have lower temperature ranges, which can be seen by the response curves of the sahelien and coast species (Fig. 8). Mild temperatures seem to be a major predictor for *Gerbillus* species richness, in conjunction with intermediate levels of precipitation. Evidently, the oceanic influence is the main responsible for the small temperature ranges on the coast (Le Houerou 1997). The areas of high potential species richness in the Sahel, though, have smaller temperature ranges due to their more equatorial location (Sayre et al. 2013). Yet, from a certain point southwards, the studied *Gerbillus* cease to exist, probably because the primary productivity reaches levels where other species competitively exclude them (Hardin et al. 1960). As such, the hypothesis that high species richness is found in areas of intermediate primary productivity (Graham & Duda 2011) is observed with *Gerbillus* in the study area. The levels of mean precipitation in the wettest quarter in the study area vary from 0 to 787 mm (Table 2). The precipitation level that is suitable for most of the species at the same time range between 170 and 200 mm (Fig. 8), which is an intermediate level from available range spectrum. Perhaps the coast of Northwest Africa would be further highlighted for species richness if considering fog as a source of primary productivity in the coastal areas (Shanyengana et al. 2002).

The real coexistence of species cannot be examined in detail with such a large scale, but in theory there are areas in the Atlantic coast and Sahel that are suitable for up to 11 species of *Gerbillus* (Fig. 13). The difference between that potential species richness and the real number of species existing in these areas should be due to competition exclusion (Hardin et al. 1960) and geographical and ecological barriers (Zink et al. 2000; Mairal et al. 2017). It would be interesting to sample the pinpointed rich areas to see how many species of *Gerbillus* really coexist there. Since ecological niches seem to be similar, strong competition is expected to exist between all species, which explains the observed temporal (Ziv et al. 1993; Wasserberg et al. 2006) and spatial segregation patterns (Ziv et al. 1993; Wasserberg et al. 2006; Traba et al. 2016). Diet is also an axis of segregation of species of similar environmental niche (van Wieren & van Langevelde

2008) but barely any study exists on *Gerbillus* with this topic (Traba et al. 2016). In this point, different floristic preferences have been suggested as potential axis of segregation at microhabitat level in *Gerbillus* (Traba et al. 2016). To verify spatial and floristic segregation, experiments have to be designed at macro and microhabitat level. Traba et al (2016) is an excellent example of such experimental design, but it only studied a species poor region with low habitat variability. A similar design could be used in Northwest Africa in a region of sharp gradient of species richness (on the coast or on Sahel), with sampling stations both in a species rich area and in a species poor area. The lower Drâa valley in Morocco seems a perfect location for such experience, as the valley seems to be rich in habitats and mammal species (Guerreiro et al. 2016), and is part of the sharp climate gradients from coast to interior desert (Brito et al. 2014).

Gerbillus pyramidum is proposed to be a dominant species over *G. henleyi* (Ziv et al. 1993; Ziv et al. 1995) but it doesn't seem to be able to occupy areas of higher levels of precipitation, as the latter species (Fig. 8). Thus, this thesis provides a first suggestion that the dominance of *G. pyramidum* over other *Gerbillus* may depend on the conditions of the environment, and it may not be able to be dominant in areas of higher primary productivity. Perhaps other rodents could take a dominant role, excluding *G. pyramidum*, but not smaller species like *G. henleyi*. Candidates for this role might be rodents of the *Meriones* or *Taterillus* genus (Granjon & Duplantier 2009). Recent studies show that *G. nigeriae* excludes *Taterillus pygargus* through competition in arid environments (Thiam et al. 2008; Thiam et al. 2011). The opposite might happen in less arid environments.

5.5 Ecological niche divergence

At last, the fourth hypothesis that the species have conserved environmental niches was corroborated on the topo-climatic and land cover axis. Even though niches are not equivalent (Identity tests, Tables 11-12), the significant background tests always showed niches to be more similar than expected for different species, and consequently the species realized niches are relatively conserved on the topo-climatic and land cover axis (Peterson et al. 1999; Warren et al. 2008; Warren et al. 2010). This niche conservatism in all considered *Gerbillus* seems to be a result of the phylogenetic inertia (Peterson et al. 1999). Nevertheless, sampling bias in species distributions delimitations can have an effect in these tests.

At a first sight, the species appear to have different responses to environmental variables, as can be seen by different weights of variables in modelling (Tables 7, 9), as well as the different response curves to climatic factors (Fig. 8). Differential climate and

habitat constraints are supposed to be a reflection of niche specialization, which should minimize competition interactions (Wasserberg et al. 2006). In the presented results, it appears that all considered gerbils have more or less the same selection of environmental variables, but are faced with different available environments in the areas where they exist (Warren et al. 2008). The exception was *G. hoogstraali*, for which the tests suggest differentiation on the climatic level. Yet, this result was considered less relevant, as it was not confirmed by tests with topo-climatic and Landover data. If the niches are relatively conserved, the reason why there are many species with different distributions is likely a result of vicariance and allopatric speciation (Kozak & Wiens 2006). Geographical vicariance seems to be particularly relevant for the coast species, with possible marine transgressions separating origin populations (Lay 1983; Lefevre & Raynal 2002). Ecological vicariance might also have played an important role, since the species realized niches appear to be conserved (Kozak & Wiens 2006; Mairal et al. 2017). Nonetheless, these results cannot be used to claim that the ecological niches of the species are the same. Ecological Niche-based modeling does not model all aspects of the species niches (Godsoe 2010). Obvious niche differences might be related to temporal and habitat segregation (Wasserberg et al. 2006; Traba et al. 2016) , which could not be addressed in the present study.

When visualizing comparisons of niche overlap between sister species (Ndiaye et al. 2012, 2016), there is no relation with phylogeny, but rather with geographical overlap. For example, sister species *G. occiduus* and *G. tarabuli* (Ndiaye et al. 2012) do not have a high geographical overlap (Tables 11-12). Gerbillus *tarabuli* has a much higher overlap with all other wide distribution species (Tables 11-12) with which shares more areas of distribution but not phylogenetic closeness (Ndiaye et al. 2012, 2016).

5.6 Variable uncertainties and spatial bias

This study constitutes the first approach of Ecological Niche Modeling of *Gerbillus* species of northwest Africa, using a considerably large number of mostly barcoded observations for several species. However, it should be made clear that there was an unavoidable spatial bias in the data, which incurred from the wideness and remoteness of parts of the study area (Brito et al. 2014). The bioclimatic variables that were used in this study were created by interpolating data measurements of weather stations throughout the world (Hijmans et al. 2005). The problem is that weather stations are rare in North Africa, which makes the data there less reliable than in other areas with multiple weather stations, as Europe (Hijmans et al. 2005). To avoid this problem, new satellite-based bioclimatic variables have been just now made available, increasing greatly the quality of variables in remote areas like the Sahara (Vega et al. 2017). However, the best existing models for past climates are based on the established knowledge (Watanabe et al. 2011; Gent et al. 2011; Giorgetta et al. 2013), and even they may not be entirely correct. Right now the ammount of rain that the Sahara received in the Middle Hollocene is being questioned, arguing it was more than previously thought (Tierney & Pausata 2017). Also the land cover variables are at the moment incomplete in North Africa, considering very broad categories like “rocky bare areas”, “sandy bare areas” and “other bare areas” (Campos et al., in press). At the moment, new land cover data with high resolution is being developed through the application of Remote Sensing techniques. (Campos et al., in press).

Even though the sampling brought numerous novel samples, these where mostly in Morocco and Mauritania, and sheer size of the study area has made it impossible to create a balanced set of samples for all species. There is a clear sampling bias favoring the Western coast of North Africa, and as well regions with less extreme climate. Some authors state that spatial bias can have serious consequences for the models, so that it isn’t the niche of the species that is being modeled, but an interaction of this niche with the distribution of the observers’ most sampled areas (Phillips et al. 2009). This bias could be responsible for the high avoidance of high temperature ranges in the models of all species (Table 8, Fig. 8), as the sampling seems to avoid areas of high temperature ranges (Brito et al. 2014). The 5x5 km spatial filtering helped dealing with clusters of samples, but it wasn’t enough to avoid clustered distributions in most species, pointed by the nearest neighbor method (Supplementary material Table S2). A complementing option could have been providing spatial bias files to maxent when modeling (Hertzog et al. 2014; Merow et al. 2016).

The results of niche comparison tests might have also been affected by sampling bias. Since the areas with most extreme temperature ranges are unsampled (Fig. 3), it is natural that all niches seem to me more similar than expected, avoiding extreme temperatures. As such, it is not exactly the niche of species that is being modeled, but an interaction of that niche with the sampling effort.

The coastal species (*G. hesperinus, G. hoogstraali, G. occiduus* and *Gerbillus sp.*) had AUC values approximate to 1, indicating that the models are overfit by such a large study area (VanDerWal et al. 2009). These models might thus be conservative, indicating smaller suitability areas than they should (VanDerWal et al. 2009), but the predicted suitabilities fit well the known distribution of the species. Perhaps the coarser pixel size (5x5 km) of the analysis attenuated the conservative effect of model overfit (Guisan et al. 2007). The models of *Gerbillus sp.* were an analytical exerciser but it behaved much like the models of the other coastal species, projecting small suitable areas on the coast.

6 Conclusions

This thesis predicts suitable areas for the 12 considered *Gerbillus* species in North Africa. Temperature variables were the most important climatic drivers of the considered species. High precipitation predicted the occurance of *G. campestris*, *G. nancillus* and *G. henleyi.* Oppositely, low precipitation predicted the occurence of *G. amoenus, G. gerbillus, G. pyramidum* and *G. tarabuli.* While some of the studied *Gerbillus* have different reactions to precipitation, they all avoid areas with high daily and annual temperature ranges. *Gerbillus gerbillus,* which seems to be the most adapted to extreme environmental conditions, avoids the areas with the highest temperature ranges, especially if it is accompanied by low minimum temperatures in the coldest month. The models of the species adapted to desert coastal ecosystems avoided high maximum temperatures in the warmest month, in what might be indirect effect of ocean fog humidity.

It was the first time that the climatic drivers of several species of *Gerbillus* were projected to the Middle Holocene, Last Glacial Maximum and Last Interglacial. Apparently, climate suitability in the humid Middle Holocene was relatively similar to the present day for all considered species. This seems to be due to the high importance of temperature ranges, which have been similar since MH. Climate suitability appears to have been generally wider in the Last Interglacial, since it was a period of slightly smaller temperature ranges in North Africa. Only with lower temperature ranges in LIG did the species distributions react to altered precipitation patterns, following or avoiding

precipitation depending on the species. Climate suitability appears to have been the lowest in the Last Glacial Maximum, when temperature ranges were the most extreme. Contrary to expectation, the models of coastal species predicted stable ranges between present day and humid Middle Holocene. This seems to have happened because the models of coastal species did not find precipitation variables to be relevant, as it was almost null in the coast, suggesting that primary productivity there is shaped by ocean humidity.

The potential species richness of *Gerbillus* seems to be predicted by low daily and annual temperature ranges and additionally intermediate precipitation levels (when considering the range of North Africa). Areas of higher species richness were pointed in the Atlantic coast of North Africa, as well as in some areas of the Sahel. It remains open how different is the predicted species richness of *Gerbillus* in those areas from the real richness of species. The difference between the two measurements should be due to factors related to species interactions, like competition, and geographical or ecological barriers. This study suggests surveying some pinpointed potential rich areas to measure the diference between potential and actual species richness.

The species environmental niches are relatively conserved. All species selected environmental variables in a similar way but they were presented with very different environments, due to the different geographic distributions. The results suggest allopatric speciation as the most probable speciation engine of the diversity observed in the genus in the region. Since the niches of the species are so similar, competition is probably a strong factor when *Gerbillus* species coexist in the same area, creating a need for segregation mechanisms on the spatial, temporal and floristic (micro-habitat) scale.

There are many species of *Gerbillus* (over 40), spanning from Northwestern Africa to India and central Asia. For stronger comparative niche studies with philogenetics, a higher number of species should be used.

In the end, most problems related to species distribution modelling could be solved with more quantity and more representativeness of sampling. Having a higher amount of diferent locations would increase the predictive power of models and allow for better spatial filtering of observations. Especially the areas with most extreme temperatures of North Africa should be surveyed to diminuish spatial bias in observations. This would finally resolve the question of if *Gerbillus* really avoid most extreme temperature ranges and lowest minimum temperatures, or if in fact it is the biologists cannot reach areas with those characteristics.

7 Bibliography

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8 Supplementary material

Table S1 Species observations used in this study.

SampleNO	Source/ GenBankID	Species	Location	Latitude	Longitude	Barcoded	Sureness
N3009	KM236112	amoenus	Niger	19.16667	7.96667	1	1
1999032	JQ753062	amoenus	Mali	18.20000	1.40000	1	1
JMD930	JQ753059	amoenus	Mauritania	18.73333	-15.6167	1	1
TES2	JQ753060	amoenus	Mali	20.20000	1.01667	1	1
TES23	JQ753061	amoenus	Mali	20.25613	0.98333	1	1
NMP48288	JQ753052	amoenus	Libya	27.23333	14.4000	1	1
79364	KT721323	amoenus	Egypt	30.40000	30.6200	1	1
86825	KT721324	amoenus	Egypt	31.06100	30.3300	1	1
101215	KT721321	amoenus	Egypt	31.58000	31.0500	1	1
1997016	AJ851270	amoenus	Mauritania	18.20000	-15.9700	1	1
ZBSC0211	Boratynsky et al., 2017	amoenus	Mauritania	21.51944	-12.8528	1	1
ZBSC0229	Boratynsky et al., 2017	amoenus	Mauritania	21.01799	-11.9249	1	1
ZBSC0239	Boratynsky et al., 2017	amoenus	Mauritania	20.26505	-13.2076	1	1
ZBSC0287	Boratynsky et al., 2017	amoenus	WesternSahara	27.15298	-10.8472	1	1
ZBSC0299	Boratynsky et al., 2017	amoenus	WesternSahara	23.57999	-15.2326	1	1
ZBSC0302	Boratynsky et al., 2017	amoenus	WesternSahara	23.28462	-15.9116	1	1
ZBSC0579	Boratynsky et al., 2017	amoenus	Morocco	31.97941	-3.70397	1	1
ZBSC0632	Boratynsky et al., 2017	amoenus	Morocco	28.84609	-10.2318	1	1
ZBSC0700	Boratynsky et al., 2017	amoenus	Morocco	28.04780	-11.3627	1	1
ZBSC0701	Boratynsky et al., 2017	amoenus	Morocco	28.10863	-11.3027	1	1
ZBSC0710	Boratynsky et al., 2017	amoenus	Morocco	28.81028	-10.4072	1	1
ZBSC0724	Boratynsky et al., 2017	amoenus	Mauritania	16.60807	-16.4365	1	1
ZBSC0800	Boratynsky et al., 2017	amoenus	Morocco	28.43926	-9.69992	1	1
ZBSC0813	Boratynsky et al., 2017	amoenus	Morocco	28.37423	-9.90223	1	1
ZBSC0883	Boratynsky et al., 2017	amoenus	Morocco	26.82801	-12.0421	1	1
18620	Boratynsky et al., 2017	amoenus	Niger	18.12000	8.78000	0	0
91-090-M-259	Boratynsky et al., 2017	amoenus	Tunisia	34.25000	9.23333	0	0
M/9804/90	Boratynsky et al., 2017	amoenus	Algeria	33.10749	1.26723	0	0
M/9805/90	Boratynsky et al., 2017	amoenus	Algeria	31.18333	-2.2500	0	0
M/9806/90	Boratynsky et al., 2017	amoenus	Algeria	30.13800	-2.1640	0	0
M/9810/90	Boratynsky et al., 2017	amoenus	Algeria	24.56667	9.48334	0	0
M/9812/90	Boratynsky et al., 2017	amoenus	Algeria	33.16673	1.58335	0	0
M/9813/90	Boratynsky et al., 2017	amoenus	Algeria	28.88999	1.97755	0	0
M/9817/90	Boratynsky et al., 2017	amoenus	Algeria	32.49058	3.71521	0	0

M/9821/90	Boratynsky et al., 2017	amoenus	Algeria	30.59118	2.89695	0	0
M/9822/90	Boratynsky et al., 2017	amoenus	Algeria	23.70008	5.13339	0	0
M/9823/90	Boratynsky et al., 2017	amoenus	Algeria	22.33335	5.55001	0	0
M/9816/90	Boratynsky et al., 2017	amoenus	Algeria	33.80000	2.90000	1	1
5035	Boratynsky et al., 2017	amoenus	Sudan	18.47600	31.83200	1	1
17243	Boratynsky et al., 2017	amoenus	Niger	18.67000	12.90000	0	1
22135	Boratynsky et al., 2017	amoenus	Tunisia	36.81000	10.18330	1	1
M5309	Boratynsky et al., 2017	amoenus	Mali	17.02640	2.11733	1	1
M5925	Boratynsky et al., 2017	amoenus	Mali	19.70972	0.00340	1	1
M5960	Boratynsky et al., 2017	amoenus	Mali	19.72278	0.18160	1	1
N3168	Boratynsky et al., 2017	amoenus	Niger	13.68333	13.30000	1	1
N3313	Boratynsky et al., 2017	amoenus	Niger	18.68333	12.91667	1	1
TES11	Boratynsky et al., 2017	amoenus	Mali	20.01523	0.94030	1	1
11586	Boratynsky et al., 2017	amoenus	WesternSahara	23.47473	-14.76096	1	1
1999030	AJ851271	campestris	Mali	18.20100	1.40000	1	1
NMP48282	KM236116	campestris	Libya	30.13333	9.48333	1	1
LG085	JN021401	campestris	Morocco	29.83333	-9.78333	1	1
LG078	JN021400	campestris	Morocco	30.06667	-9.65833	1	1
26BH	GU356565	campestris	Tunisia	34.48333	9.65000	1	1
6HM	GU356567	campestris	Tunisia	36.33333	10.50000	1	1
1999040	KF496218	campestris	Niger	16.96667	7.98306	1	1
2002278	KC835915	campestris	Niger	18.47000	4.78000	1	1
CBGB-TES38	KC835919	campestris	Mali	20.20000	1.01000	1	1
2003002	KC835916	campestris	Morocco	26.12000	-13.53000	1	1
LG061	KC835907	campestris	Morocco	30.40000	-8.92000	1	1
LG058	KC835905	campestris	Morocco	30.41000	-8.90000	1	1
LG053	KC835903	campestris	Morocco	31.32000	-9.71000	1	1
LG026	KC835890	campestris	Morocco	31.47000	-9.76000	1	1
MOHMIE-MA845	KC835846	campestris	Morocco	31.54000	-8.99000	1	1
LG002	KC835868	campestris	Morocco	31.82000	-7.97000	1	1
MOHMIE-MA855	KC835848	campestris	Morocco	31.84000	-7.01000	1	1
MOHMIE-OTE01	KC835918	campestris	Morocco	32.45000	-8.15000	1	1
MOHMIE-MA946	KC835853	campestris	Morocco	33.42000	-5.04000	1	1
MOHMIE-ST2A17b	KC835860	campestris	Morocco	33.60000	-7.13000	1	1
MOHMIE-SB22	KC835857	campestris	Morocco	34.24000	-6.67000	1	1
TASSILI-119	KC835863	campestris	Algeria	34.30000	2.97000	1	1
MOHMIE-MA220	KC835831	campestris	Morocco	34.52000	-2.02000	1	1
MOHMIE-MA745	KC835844	campestris	Morocco	34.82000	-6.29000	1	1
1997064	KC835911	campestris	Tunisia	35.03000	9.50000	1	1

MOHMIE-MA660	KC835835	campestris	Morocco	35.37000	-5.17000	1	1
MOHMIE-MA477	KC835833	campestris	Morocco	35.53000	-5.53000	1	1
ZBSC0739	Boratynsky et al., 2017	campestris	Mauritania	15.90402	-11.93626	1	1
ZBSC0348	Boratynsky et al., 2017	campestris	Mauritania	16.44429	-11.7780	1	1
ZBSC0055	Boratynsky et al., 2017	campestris	Mauritania	17.16204	-12.1281	1	1
ZBSC0489	Boratynsky et al., 2017	campestris	Mauritania	17.58916	-7.44597	0	1
ZBSC0259	Boratynsky et al., 2017	campestris	Mauritania	17.88809	-12.1151	1	1
ZBSC0264	Boratynsky et al., 2017	campestris	Mauritania	18.05357	-11.9440	1	1
ZBSC0494	Boratynsky et al., 2017	campestris	Mauritania	18.09958	-8.01073	0	1
ZBSC0564	Boratynsky et al., 2017	campestris	Mauritania	18.15051	-12.0657	0	1
ZBSC0555	Boratynsky et al., 2017	campestris	Mauritania	18.20623	-11.7303	0	1
ZBSC0507	Boratynsky et al., 2017	campestris	Mauritania	18.36747	-9.04853	0	1
ZBSC0551	Boratynsky et al., 2017	campestris	Mauritania	18.40035	-11.8146	1	1
ZBSC0529	Boratynsky et al., 2017	campestris	Mauritania	18.44282	-11.3874	0	1
ZBSC0534	Boratynsky et al., 2017	campestris	Mauritania	18.44282	-11.3874	1	1
ZBSC0238	Boratynsky et al., 2017	campestris	Mauritania	20.26505	-13.2076	1	1
ZBSC0225	Boratynsky et al., 2017	campestris	Mauritania	20.55080	-12.6762	1	1
ZBSC0233	Boratynsky et al., 2017	campestris	Mauritania	21.01799	-11.9249	1	1
ZBSC0217	Boratynsky et al., 2017	campestris	Mauritania	21.43810	-12.9800	1	1
ZBSC0216	Boratynsky et al., 2017	campestris	Mauritania	21.77516	-12.8794	1	1
ZBSC0416	Boratynsky et al., 2017	campestris	WesternSahara	22.61107	-14.4709	0	1
ZBSC0649	Boratynsky et al., 2017	campestris	Morocco	28.25845	-11.5354	1	1
ZBSC0798	Boratynsky et al., 2017	campestris	Morocco	28.42764	-9.70043	1	1
ZBSC0799	Boratynsky et al., 2017	campestris	Morocco	28.44669	-9.70331	1	1
ZBSC0390	Boratynsky et al., 2017	campestris	Morocco	28.45413	-10.05126	0	1
8068	Boratynsky et al., 2017	campestris	Morocco	28.66393	-10.65669	0	1
8066	Boratynsky et al., 2017	campestris	Morocco	28.98554	-10.29129	0	1
ZBSC0639	Boratynsky et al., 2017	campestris	Morocco	30.43337	-8.89323	1	1
8083	Boratynsky et al., 2017	campestris	Morocco	30.73865	-6.65121	0	1
17240	Boratynsky et al., 2017	campestris	Niger	19.09800	12.91600	1	1
17005	Boratynsky et al., 2017	campestris	Sudan	21.83100	24.98500	0	0
37777	Boratynsky et al., 2017	campestris	Sudan	21.83500	25.01900	1	1
17002	Boratynsky et al., 2017	campestris	Libya	21.96300	24.82000	1	1
37778	Boratynsky et al., 2017	campestris	Egypt	22.03725	25.09651	0	0
M/9118/89	Boratynsky et al., 2017	campestris	Algeria	22.89755	5.37775	0	0
M/9116/89	Boratynsky et al., 2017	campestris	Algeria	23.13129	5.74307	0	0

25748	Boratynsky et al., 2017	campestris	Algeria	23.30000	5.68400	0	0
M/9114/89	Boratynsky et al., 2017	campestris	Algeria	23.70008	5.13339	0	0
M/9058/89	Boratynsky et al., 2017	campestris	Algeria	24.47132	9.68200	0	0
M/9067/89	Boratynsky et al., 2017	campestris	Algeria	24.48337	9.70003	0	0
M/9072/89	Boratynsky et al., 2017	campestris	Algeria	24.56667	9.48334	0	0
M/9051/89	Boratynsky et al., 2017	campestris	Algeria	24.64800	9.62900	0	0
M/9057/89	Boratynsky et al., 2017	campestris	Algeria	24.67300	9.72900	0	0
25768	Boratynsky et al., 2017	campestris	Libya	24.91100	17.75900	1	1
M/9113/89	Boratynsky et al., 2017	campestris	Algeria	25.00000	4.33333	0	0
M/9119/89	Boratynsky et al., 2017	campestris	Algeria	25.30000	3.73360	0	0
M/9120/89	Boratynsky et al., 2017	campestris	Algeria	26.00001	3.50001	1	1
M/9087/89	Boratynsky et al., 2017	campestris	Algeria	26.71668	0.16670	0	0
M/9111/89	Boratynsky et al., 2017	campestris	Algeria	28.01600	2.66700	0	0
M/9045/89	Boratynsky et al., 2017	campestris	Algeria	30.13800	-2.16400	0	0
M/9110/89	Boratynsky et al., 2017	campestris	Algeria	30.59118	2.89695	0	0
15189	Boratynsky et al., 2017	campestris	Libya	30.82000	14.28000	1	1
M/9100/89	Boratynsky et al., 2017	campestris	Algeria	30.91668	-2.03334	0	0
28086	Boratynsky et al., 2017	campestris	Morocco	31.15000	-7.45000	0	0
17239	Boratynsky et al., 2017	campestris	Algeria	32.00010	5.26660	0	0
91-090-M-288	Boratynsky et al., 2017	campestris	Libya	32.50000	20.83000	1	1
28088	Boratynsky et al., 2017	campestris	Morocco	32.54000	-9.27000	0	0
30262	Boratynsky et al., 2017	campestris	Libya	32.68400	21.60000	0	0
30255	Boratynsky et al., 2017	campestris	Libya	32.76700	21.33400	0	0
27347	Boratynsky et al., 2017	campestris	Libya	32.81700	21.51700	0	0
21983	Boratynsky et al., 2017	campestris	Tunisia	33.00100	11.24800	1	1
M/9048/89	Boratynsky et al., 2017	campestris	Algeria	33.10749	1.26723	0	0
28090	Boratynsky et al., 2017	campestris	Morocco	33.80000	-7.16667	0	0
22131	Boratynsky et al., 2017	campestris	Tunisia	33.88000	10.85000	0	0
91-090-M-262	Boratynsky et al., 2017	campestris	Tunisia	33.88333	10.11667	0	0
M/9125/89	Boratynsky et al., 2017	campestris	Algeria	34.16668	0.08335	0	0
M/9079/89	Boratynsky et al., 2017	campestris	Algeria	35.16660	-1.65010	0	0
M/9127/89	Boratynsky et al., 2017	campestris	Algeria	35.21667	-0.75000	0	0
M/9095/89	Boratynsky et al., 2017	campestris	Algeria	35.45000	-0.01667	0	0
M/9044/89	Boratynsky et al., 2017	campestris	Algeria	35.48335	-0.51668	0	0
M/9094/89	Boratynsky et al., 2017	campestris	Algeria	35.59305	-0.41468	0	0
M/9091/89	Boratynsky et al., 2017	campestris	Algeria	35.64000	-0.77000	0	0

M/9129/89	Boratynsky et al., 2017	campestris	Algeria	35.66600	-0.99900	0	0
21980	Boratynsky et al., 2017	campestris	Tunisia	36.18000	8.72000	0	0
21967	Boratynsky et al., 2017	campestris	Tunisia	36.40000	10.61600	0	0
M/9041/89	Boratynsky et al., 2017	campestris	Algeria	36.42650	2.75764	1	1
22133	Boratynsky et al., 2017	campestris	Tunisia	36.80000	10.18330	0	0
22023	Boratynsky et al., 2017	campestris	Tunisia	36.94000	10.19000	0	0
91-090-M-256	Boratynsky et al., 2017	campestris	Tunisia	37.08300	9.85000	0	0
21969	Boratynsky et al., 2017	campestris	Tunisia	37.20000	9.70000	0	0
88F	GU356564	gerbillus	Tunisia	33.16000	8.29000	1	1
GGE1/99-280 (fini)	AJ851269	gerbillus	Mauritania	18.10000	-16.00000	1	1
1997012	KM236123	gerbillus	Algeria	30.06667	2.08333	1	1
1997015	KM236122	gerbillus	Egypt	25.70000	28.88333	1	1
M5928	KM236125	gerbillus	Mali	19.31667	0.23333	1	1
S10465	KM236121	gerbillus	Mauritania	16.55309	-16.2335	1	1
GeGerb1	JN652802	gerbillus	Niger	19.01000	11.43000	1	1
BM113	Ndiaye et al. 2012	gerbillus	Mauritania	22.08000	-12.4100	1	1
Ge.-Gerb1	JN652802	gerbillus	Niger	19.01667	11.71667	1	1
LG124	JN021409	gerbillus	Morocco	27.96667	-12.78333	1	1
1999280	LN606679	gerbillus	Mauritania	18.33333	-15.9667	1	1
M4953	KF496219	gerbillus	Mali	19.35000	0.18333	1	1
101113	KT721331	gerbillus	Egypt	31.57000	25.15000	1	1
101162	KT721333	gerbillus	Egypt	30.25000	28.92000	1	1
8077	Boratynsky et al., 2017	gerbillus	Morocco	26.69416	-11.7909	1	1
ZBSC0065	Boratynsky et al., 2017	gerbillus	Mauritania	18.91943	-15.38496	1	1
ZBSC0075	Boratynsky et al., 2017	gerbillus	Mauritania	20.47167	-15.60663	0	1
ZBSC0205	Boratynsky et al., 2017	gerbillus	Mauritania	21.24881	-14.46077	0	1
ZBSC0266	Boratynsky et al., 2017	gerbillus	Mauritania	20.86302	-16.16268	0	1
ZBSC0304	Boratynsky et al., 2017	gerbillus		20.37572	-15.99117	0	1
ZBSC0305	Boratynsky et al., 2017	gerbillus		20.09920	-15.92696	0	1
ZBSC0402	Boratynsky et al., 2017	gerbillus	Morocco	27.84463	-12.91416	0	1
ZBSC0490	Boratynsky et al., 2017	gerbillus	Mauritania	17.58916	-7.44597	0	1
ZBSC0492	Boratynsky et al., 2017	gerbillus	Mauritania	18.09958	-8.01073	0	1
ZBSC0496	Boratynsky et al., 2017	gerbillus	Mauritania	18.38080	-8.27220	0	1
ZBSC0504	Boratynsky et al., 2017	gerbillus	Mauritania	18.36747	-9.04853	0	1
ZBSC0513	Boratynsky et al., 2017	gerbillus	Mauritania	18.57872	-9.81861	0	1
ZBSC0556	Boratynsky et al., 2017	gerbillus	Mauritania	18.20623	-11.73033	0	1
ZBSC0572	Boratynsky et al., 2017	gerbillus	Mauritania	20.73042	-16.02483	0	1
ZBSC0418	Boratynsky et al., 2017	gerbillus		20.84449	-16.14882	1	1

ZBSC0573	Boratynsky et al., 2017	gerbillus		20.73042	-16.02483	1	1
ZBSC0659	Boratynsky et al., 2017	gerbillus	Morocco	27.76312	-12.92827	1	1
ZBSC0680	Boratynsky et al., 2017	gerbillus	Morocco	26.86599	-11.71810	1	1
ZBSC0753	Boratynsky et al., 2017	gerbillus	Mauritania	18.88088	-15.44537	1	1
ZBSC0763	Boratynsky et al., 2017	gerbillus	Mauritania	19.07167	-15.05007	1	1
ZBSC0784	Boratynsky et al., 2017	gerbillus	Morocco	27.92608	-12.46731	1	1
ZBSC0071	Boratynsky et al., 2017	gerbillus	Mauritania	20.61124	-16.01271	1	1
ZBSC0073	Boratynsky et al., 2017	gerbillus	Mauritania	19.85158	-15.64683	1	1
ZBSC0201	Boratynsky et al., 2017	gerbillus	Mauritania	21.28029	-16.09178	1	1
ZBSC0208	Boratynsky et al., 2017	gerbillus	Mauritania	21.19749	-14.22212	1	1
ZBSC0212	Boratynsky et al., 2017	gerbillus	Mauritania	21.51944	-12.85283	1	1
ZBSC0227	Boratynsky et al., 2017	gerbillus	Mauritania	21.37281	-11.91046	1	1
ZBSC0250	Boratynsky et al., 2017	gerbillus	Mauritania	19.74006	-16.27462	1	1
ZBSC0297	Boratynsky et al., 2017	gerbillus	WesternSahara	23.78419	-14.79388	1	1
ZBSC0298	Boratynsky et al., 2017	gerbillus	WesternSahara	23.57999	-15.23256	1	1
ZBSC0301	Boratynsky et al., 2017	gerbillus	WesternSahara	23.25687	-15.88736	1	1
8247	Boratynsky et al., 2017	gerbillus	Sudan	21.76667	31.28333	0	0
12064	Boratynsky et al., 2017	gerbillus	Libya	24.20000	23.10000	0	0
22136	Boratynsky et al., 2017	gerbillus	Tunisia	36.43330	10.58300	0	0
30219	Boratynsky et al., 2017	gerbillus	Libya	32.76667	21.33333	0	0
91-090-M-228	Boratynsky et al., 2017	gerbillus	Tunisia	30.50000	9.25000	0	0
91-090-M-257	Boratynsky et al., 2017	gerbillus	Tunisia	37.00000	10.16667	0	0
17021	Boratynsky et al., 2017	gerbillus	Libya	21.96000	25.13000	0	0
17024	Boratynsky et al., 2017	gerbillus	Egypt	22.03725	25.09651	0	0
17025	Boratynsky et al., 2017	gerbillus	Libya	22.01100	24.96000	0	0
17230	Boratynsky et al., 2017	gerbillus	Niger	21.01600	12.30100	0	0
17231	Boratynsky et al., 2017	gerbillus	Algeria	33.88300	7.36600	0	0
17232	Boratynsky et al., 2017	gerbillus	Algeria	33.33300	6.88330	0	0
17908	Boratynsky et al., 2017	gerbillus	Libya	30.78000	17.83000	0	0
25759	Boratynsky et al., 2017	gerbillus	Libya	24.91100	17.75900	0	0
30221	Boratynsky et al., 2017	gerbillus	Libya	30.45000	18.48333	0	0
37808	Boratynsky et al., 2017	gerbillus	Egypt	22.03823	25.20108	0	0
91-090-M-217	Boratynsky et al., 2017	gerbillus	Tunisia	33.16000	10.33000	0	0
M/9136/89	Boratynsky et al., 2017	gerbillus	Algeria	29.00000	-0.25000	0	0
M/9158/89	Boratynsky et al., 2017	gerbillus	Algeria	31.18333	-2.25000	0	0
M/9163/89	Boratynsky et al., 2017	gerbillus	Algeria	30.13800	-2.16400	0	0

M/9169/89	Boratynsky et al., 2017	gerbillus	Algeria	24.47132	9.68200	0	0
M/9171/89	Boratynsky et al., 2017	gerbillus	Algeria	24.48300	9.69900	0	0
M/9175/89	Boratynsky et al., 2017	gerbillus	Algeria	24.56667	9.48334	0	0
M/9191/89	Boratynsky et al., 2017	gerbillus	Algeria	29.66600	-1.66800	0	0
M/9195/89	Boratynsky et al., 2017	gerbillus	Algeria	26.71668	0.16670	0	0
M/9200/89	Boratynsky et al., 2017	gerbillus	Algeria	28.88999	1.97755	0	0
M/9205/89	Boratynsky et al., 2017	gerbillus	Algeria	30.71667	3.13333	0	0
M/9207/89	Boratynsky et al., 2017	gerbillus	Algeria	33.10749	1.26723	0	0
M/9217/88	Boratynsky et al., 2017	gerbillus	Algeria	28.01667	2.66668	0	0
M/9218/89	Boratynsky et al., 2017	gerbillus	Algeria	26.50020	3.05002	0	0
M/9219/89	Boratynsky et al., 2017	gerbillus	Algeria	25.00000	4.33333	0	0
M/9227/89	Boratynsky et al., 2017	gerbillus	Algeria	23.70008	5.13339	0	0
M/9229/89	Boratynsky et al., 2017	gerbillus	Algeria	22.33335	5.55001	0	0
M/9235/89	Boratynsky et al., 2017	gerbillus	Algeria	25.30000	3.73360	0	0
M/9237/89	Boratynsky et al., 2017	gerbillus	Algeria	26.00001	3.50001	0	0
5044	Boratynsky et al., 2017	gerbillus	Egypt	29.16250	33.62639	1	1
8248	Boratynsky et al., 2017	gerbillus	Sudan	22.12000	31.32000	1	1
25754	Boratynsky et al., 2017	gerbillus	Libya	25.90000	13.85000	1	1
M/9192/89	Boratynsky et al., 2017	gerbillus	Algeria	28.25002	-0.20001	1	1
M5938	Boratynsky et al., 2017	gerbillus	Mali	17.82325	-3.19743	1	1
M5947	Boratynsky et al., 2017	gerbillus	Mali	19.33048	-0.23362	1	1
M5957	Boratynsky et al., 2017	gerbillus	Mali	19.70972	0.00340	1	1
M5976	Boratynsky et al., 2017	gerbillus	Mali	19.74620	-0.03402	1	1
M5985	Boratynsky et al., 2017	gerbillus	Mali	19.35568	-0.24178	1	1
N3035	Boratynsky et al., 2017	gerbillus	Niger	18.55000	7.78333	1	1
	Hadjoudj et al., 2015	Gerbilus	Algeria	32.94486	6.26065	1	1
2002487	LN606682	henleyi	Tanout, Niger	14.85000	8.88333	1	1
AD1054	KF496233	henleyi	Dodel, Senegal	16.47875	-14.4509	1	1
KOR8	KF496227	henleyi	Gangara, Niger	14.36399	8.29882	1	1
M4058	KF496221	henleyi	Makana, Mali	15.16333	-9.49583	1	1
M4947	KF496223	henleyi	Tedouft, Mali	15.91600	2.46000	1	1
M5597	KF496220	henleyi	Markoye, Burkina Faso	14.62417	0.04320	1	1
MAD355	KF496222	henleyi	DianbÚ, Mali	14.59888	-5.92670	1	1
N3272	KF496229	henleyi	Tanout, Niger	14.95000	8.88333	1	1
N4291	KF496224	henleyi	Gangara, Niger	14.61700	8.52002	1	1
N4293	KF496226	henleyi	Gangara, Niger	14.62470	8.49928	1	1
N3307		henleyi	Niger	14.26667	0.73333		1
1999037		henleyi	Niger	14.84917	2.68417		0

N3238		henleyi	Niger	16.55000	7.13330		0
S2020		henleyi	Senegal	16.46667	-15.70000		0
ZBSC0369	Boratynsky et al., 2017	henleyi	Mauritania	16.76294	-11.22198	1	1
ZBSC0067	Boratynsky et al., 2017	henleyi	Mauritania	19.80879	-14.28847	1	1
M/9703/90	Boratynsky et al., 2017	henleyi	Algeria	35.08957	3.02987	1	1
1981019	JN652803	hesperinus	S Essaouira, Morocco	31.46667	-9.75000		1
LG065	JN021412	hoogstrali	Oued Souss, Morocco	30.41667	-8.90000	1	1
1997046	KF496257	nancillus	Niger	13.48333	7.10000	1	1
1999041	KF496253	nancillus	Niger	14.84917	2.68417	1	1
1999051	KF496242	nancillus	Niger	15.04167	2.70360	1	1
1999060	KF496259	nancillus	Niger	14.95000	2.71667	1	1
AD2205	KF496241	nancillus	Molodo, Mali	14.20932	-6.14703	1	1
KB8469	KF496264	nancillus	Dodel, Senegal	16.48190	-14.4713	1	1
KOR12	KF496251	nancillus	Gangara, Niger	14.36403	8.29886	1	1
M4067	KF496237	nancillus	Mali	15.18348	-9.52768	1	1
M4072	KF496239	nancillus	Mali	15.01882	-7.66807	1	1
MAD341	KF496238	nancillus	Mali	14.62583	-5.89612	1	1
N3089	KF496260	nancillus	Niger	14.50000	3.23000	1	1
N3207	KF496256	nancillus	Niger	13.35000	2.28333	1	1
NGAN193	KF496246	nancillus	Niger	14.61028	8.50000	1	1
NGAN64	KF496244	nancillus	Niger	14.60685	8.51792	1	1
SKB7362	KF496276	nancillus	Senegal	15.85438	-15.06295	1	1
SKB7435	KF496269	nancillus	Senegal	15.84150	-14.8112	1	1
SKB7465	KF496278	nancillus	Senegal	15.82000	-15.0700	1	1
ZBSC0058	Boratynsky et al., 2017	nancillus	Mauritania	17.42283	-13.43516	1	1
	AJ430555	nigeriae	Niger	13.60000	2.10000	1	0
	Diatta et al., 2015	nigeriae	Nigeria,Tiloa	15.09000	2.04000	0	0
	Diatta et al., 2015	nigeriae	Nigeria, Tékhé	14.01000	6.01000	0	0
	Diatta et al., 2015	nigeriae	Mali, Hassilbarké-Maure	14.54000	-9.24000	0	0
19971471	KM236135	nigeriae	Mauritania	19.59972	-16.4319	1	1
KEL3	KM236138	nigeriae	Niger	14.26674	10.10007	1	1
LAC27	KM236134	nigeriae	Chad	12.83333	14.75000	1	1
M4606	KM236136	nigeriae	Mali	15.99428	-4.18622	1	1
SKB3764	KM236137	nigeriae	Senegal	15.15110	-16.6058	1	1
	AF141226	nigeriae	Kiji, Mauritania	19.70000	-16.5000	1	1
1995046	LN606688	nigeriae	Mauritania	16.36417	-16.4685	1	1
2002281	LN606687	nigeriae	Niger	14.73333	0.91667	1	1
N2676	KF496280	nigeriae	Niger	13.16667	4.08333	1	1
NGAN115	KF496281	nigeriae	Niger	14.60962	8.51008	1	1
ZBSC0030	Boratynsky et al. 2017	nigeriae	Mauritania	16.43478	-14.03688	0	1
ZBSC0060	Boratynsky et al. 2017	nigeriae	Mauritania	17.42283	-13.43516	1	1

ZBSC0248	Boratynsky et al. 2017	nigeriae	Mauritania	19.85133	-16.35772	1	1
ZBSC0322	Boratynsky et al. 2017	nigeriae	Mauritania	15.99944	-11.87261	1	1
ZBSC0339	Boratynsky et al. 2017	nigeriae	Mauritania	16.05328	-11.66993	1	1
ZBSC0370	Boratynsky et al. 2017	nigeriae	Mauritania	16.76294	-11.22198	1	1
ZBSC0477	Boratynsky et al. 2017	nigeriae		15.94034	-9.45654	1	1
M5972	Boratynsky et al. 2017	nigeriae	Mali	19.72118	-0.02867	1	1
LG103	JN021421	occiduus	Morocco	28.84147	-10.8458	1	1
LG110	JN021432	occiduus	Morocco	28.48162	-11.2375	1	1
LG115	JN021440	occiduus	Morocco	27.95602	-12.7607	1	1
LG119	JN021438	occiduus	Morocco	27.96267	-12.8333	1	1
MAK8	JN652805	occiduus	Morocco	26.13333	-14.4890	1	1
2002226	LN606689	occiduus	Morocco	28.46670	-11.1000	1	1
ZBSC0018	Boratynsky et al. 2017	occiduus	Morocco	25.40455	-14.75259	0	1
ZBSC0407	Boratynsky et al. 2017	occiduus		23.84568	-15.84750	1	1
ZBSC0410	Boratynsky et al. 2017	occiduus		23.83728	-15.71086	1	1
ZBSC0617	Boratynsky et al. 2017	occiduus	Morocco	28.17284	-11.87186	1	1
ZBSC0619	Boratynsky et al. 2017	occiduus	Morocco	27.97408	-12.50536	1	1
ZBSC0625	Boratynsky et al. 2017	occiduus	Morocco	28.06763	-12.14309	1	1
ZBSC0658	Boratynsky et al. 2017	occiduus	Morocco, Tarfaya	27.88164	-12.88003	1	1
LG135	Boratynsky et al. 2017	occiduus	Morocco	23.88507	-15.83008	0	1
M5978	KM236141	pyramidum	Mali	19.35000	-0.23333	1	1
S10334	KM236140	pyramidum	Mauritania	19.73606	-14.36742	1	1
AKJmau7	JN652811	pyramidum	Akjoujt, Mauritania	16.73333	-14.36667	1	1
CHAmal1	JN652809	pyramidum	Mali	19.71667	-0.01667	1	1
Ge.-Pyra1	JN652807	pyramidum	Niger	18.11667	11.58333	1	1
GOUnig	JN652813	pyramidum	Niger	18.55000	7.78333	1	1
JEZlib2	JN652808	pyramidum	Jezero Gabroon, Lybia	27.05000	14.43333	1	1
MENmal	JN652812	pyramidum	Mali	15.90000	2.41667	1	1
SOUmau	JN652810	pyramidum	Mauritania	20.26667	-13.11667	1	1
1998086	LN606691	pyramidum	Niger	17.00000	8.00000	1	1
2002300	KF496283	pyramidum	Chad	16.46667	15.61667	1	1
100058	Ndiaye et al. 2016	pyramidum	Egypt	27.17000	32.27000	1	0
35321	KT721344	pyramidum	Sudan	19.58000	37.01000	1	1
82322	KT721345	pyramidum	Egypt	22.18000	36.35000	1	1
82339	KT721346	pyramidum	Egypt	22.22000	36.63000	1	1
87628	KT721357	pyramidum	Egypt	27.25000	30.58000	1	1
100056	KT721355	pyramidum	Egypt	30.03000	31.10000	1	1
100073	KT721350	pyramidum	Egypt	30.40000	31.60000	1	1
100088	KT721356	pyramidum	Egypt	24.08000	32.88000	1	1
106119	KT721351	pyramidum	Egypt	28.35000	28.87000	1	1

106268	KT721352	pyramidum	Egypt	22.83000	35.77000	1	1
106278	KT721353	pyramidum	Egypt	25.48000	28.98000	1	1
107172	KT721354	pyramidum	Mauritania	28.48000	29.03000	1	1
ZBSC0066	Boratynsky et al. 2017	pyramidum	Mauritania	19.80879	-14.28847	0	1
ZBSC0593	Boratynsky et al. 2017	pyramidum	Morocco	32.25735	-2.24072	0	1
ZBSC0234	Boratynsky et al. 2017	pyramidum	Mauritania	21.01799	-11.92489	1	1
5043	Boratynsky et al. 2017	pyramidum	Egypt	29.90000	31.40000	0	0
5048	Boratynsky et al. 2017	pyramidum	Sudan	15.52000	32.59600	0	0
5049	Boratynsky et al. 2017	pyramidum	Sudan	19.66000	30.43910	0	0
18622	Boratynsky et al. 2017	pyramidum	Niger	18.58300	8.78300	0	0
18623	Boratynsky et al. 2017	pyramidum	Niger	18.12000	8.78000	0	0
22134	Boratynsky et al. 2017	pyramidum	Tunisia	36.80000	10.18330	0	0
25751	Boratynsky et al. 2017	pyramidum	Libya	25.90000	13.85000	0	0
91-090-M-215	Boratynsky et al. 2017	pyramidum	Tunisia	36.44000	10.58000	0	0
91-090-M-216	Boratynsky et al. 2017	pyramidum	Tunisia	37.00010	10.16660	0	0
M5185	Boratynsky et al. 2017	pyramidum	Mali	17.22717	0.24100	0	0
8249	Boratynsky et al. 2017	pyramidum	Sudan	22.12000	31.32000	1	1
M5937	Boratynsky et al. 2017	pyramidum	Mali	19.72790	0.19118	1	1
M5942	Boratynsky et al. 2017	pyramidum	Mali	20.01523	0.94030	1	1
M5978	Boratynsky et al. 2017	pyramidum	Mali	19.33782	-0.24033	1	1
M6108	Boratynsky et al. 2017	pyramidum	Senegal	18.03032	0.47515	1	1
M6133	Boratynsky et al. 2017	pyramidum	Senegal	19.41282	-0.57765	1	1
N3008	Boratynsky et al. 2017	pyramidum	Niger	19.16667	7.96667	1	1
N3015	Boratynsky et al. 2017	pyramidum	Niger	17.41667	6.78333	1	1
N3036	Boratynsky et al. 2017	pyramidum	Niger	17.45000	6.70000	1	1
N3039	Boratynsky et al. 2017	pyramidum	Niger	18.93333	8.25000	1	1
N3073	Boratynsky et al. 2017	pyramidum	Chad	13.46742	14.71270	1	1
N3329	Boratynsky et al. 2017	pyramidum	Niger	15.63333	11.51667	1	1
TES28	Boratynsky et al. 2017	pyramidum	Mali	20.19423	0.97225	1	1
LG079	JN021446	sp.	Souss Massa NP, Morocco	30.06667	-9.65833	1	1
LG090	JN021447	sp.	Aglou, Morocco	29.80000	-9.83333	0	1
ZBSC0634	Boratynsky et al. 2017	sp.	Morocco	29.81200	-9.79036	1	1
ZBSC0638	Boratynsky et al. 2017	sp.	Morocco	29.82627	-9.78467	1	1
10628	Boratynsky et al. 2017	sp.	Morocco, Douira	29.51800	-11.28700	0	1
10628	Boratynsky et al. 2017	sp.	Morocco, Douira	28.51200	-11.29710	1	1
5D	GU356572	tarabuli	Dghoumes, Tunisia	34.04000	8.56000	0	1
86F	GU356571	tarabuli	Faouar, Tunisia	33.16000	8.29000	0	1

	Hadjoudj et al., 2015	Tarabuli	Algeria	32.94486	6.26065	0	0
2000010	KM236146	tarabuli	Senegal	16.46667	-15.75000	1	1
M4622	KM236143	tarabuli	Mali	15.93333	-3.96667	1	1
AGAnig**	JN652822	tarabuli	Niger	17.00000	7.93333	1	1
AGNmau**	JN652815	tarabuli	Mauritania	19.33333	-16.28333	1	1
AKJmau**	JN652826	tarabuli	Mauritania	16.73333	-14.36667	1	1
AYOmau3**	JN652817	tarabuli	Mauritania	16.58333	-9.58333	1	1
BENalg3**	JN652821	tarabuli	Algeria	30.06667	-2.08333	1	1
KABmal2**	JN652828	tarabuli	Mali	16.71667	-2.98333	1	1
KREmal1	JN652831	tarabuli	Mali	19.35000	0.18333	1	1
MAK6	JN652798	tarabuli	Morocco	23.89128	-14.53333	1	1
MOUmau1**	JN652827	tarabuli	Mauritania	17.21667	-16.11667	1	1
TEGnig2	JN652825	tarabuli	Niger	17.45000	6.70000	1	1
TIDmal1	JN652829	tarabuli	Mali	17.01667	2.11667	1	1
TOMmal2	JN652830	tarabuli	Mali	16.75000	2.98333	1	1
1999669	LN606696	tarabuli	Niger	14.51667	3.30000	1	1
2002403	LN606697	tarabuli	Niger	14.25000	13.15000	1	1
MAK24	KF496285	tarabuli	Morocco	31.29123	-4.32447	1	1
8074	Boratynsky et a.,l 2017	tarabuli	Morocco	26.80498	-11.73927	0	1
8075	Boratynsky et a.,l 2017	tarabuli	Morocco	26.57773	-12.07124	0	1
ZBSC0023	Boratynsky et a.,l 2017	tarabuli	Mauritania	17.03159	-16.27258	0	1
ZBSC0031	Boratynsky et a.,l 2017	tarabuli	Mauritania	16.43478	-14.03688	0	1
ZBSC0039	Boratynsky et a.,l 2017	tarabuli	Mauritania	15.64185	-12.10998	0	1
ZBSC0078	Boratynsky et a.,l 2017	tarabuli	Mauritania	20.56131	-16.01397	0	1
ZBSC0252	Boratynsky et a.,l 2017	tarabuli	Mauritania	18.79511	-16.13898	0	1
ZBSC0255	Boratynsky et a.,l 2017	tarabuli	Mauritania	17.57850	-12.88109	0	1
ZBSC0381	Boratynsky et a.,l 2017	tarabuli		20.69251	-16.03900	0	1
ZBSC0486	Boratynsky et a.,l 2017	tarabuli	Mauritania	16.48414	-9.28959	0	1
ZBSC0592	Boratynsky et a.,l 2017	tarabuli	Morocco	32.25396	-2.18788	0	1
ZBSC0495	Boratynsky et a.,l 2017	tarabuli		18.38080	-8.27220	1	1
ZBSC0518	Boratynsky et a.,l 2017	tarabuli		18.44719	-10.68334	1	1
ZBSC0623	Boratynsky et a.,l 2017	tarabuli	Morocco	27.90755	-12.36816	1	1
ZBSC0624	Boratynsky et a.,l 2017	tarabuli	Morocco	28.00437	-12.24112	1	1
ZBSC0644	Boratynsky et a.,l 2017	tarabuli	Morocco	28.23131	-11.51164	1	1
ZBSC0664	Boratynsky et a.,l 2017	tarabuli	Morocco	27.25337	-12.80658	1	1
ZBSC0677	Boratynsky et a.,l 2017	tarabuli	Morocco	26.86325	-11.75480	1	1
ZBSC0752	Boratynsky et a.,l 2017	tarabuli	Mauritania	18.82637	-15.49242	1	1
ZBSC0762	Boratynsky et a.,l 2017	tarabuli	Mauritania	19.16755	-14.97378	1	1

ZBSC0817	Boratynsky et a.,l 2017	tarabuli	Morocco	28.37838	-9.87954	1	1
ZBSC0885	Boratynsky et a.,l 2017	tarabuli	Morocco	26.82801	-12.04209	1	1
ZBSC0059	Boratynsky et a.,l 2017	tarabuli	Mauritania	17.42283	-13.43516	1	1
ZBSC0068	Boratynsky et a.,l 2017	tarabuli	Mauritania	20.55489	-16.15536	1	1
ZBSC0204	Boratynsky et a.,l 2017	tarabuli	Mauritania	21.28029	-16.09178	1	1
ZBSC0215	Boratynsky et a.,l 2017	tarabuli	Mauritania	21.51944	-12.85283	1	1
ZBSC0230	Boratynsky et a.,l 2017	tarabuli	Mauritania	21.01799	-11.92489	1	1
ZBSC0254	Boratynsky et a.,l 2017	tarabuli	Mauritania	17.36391	-13.57210	1	1
ZBSC0282	Boratynsky et a.,l 2017	tarabuli	Morocco	29.54062	-8.02484	1	1
ZBSC0284	Boratynsky et a.,l 2017	tarabuli	Morocco	28.75829	-9.12675	1	1
ZBSC0285	Boratynsky et a.,l 2017	tarabuli	Morocco	27.92163	-10.00074	1	1
ZBSC0288	Boratynsky et a.,l 2017	tarabuli	WesternSahara	27.15348	-10.84721	1	1
M5383	Boratynsky et a.,l 2017	tarabuli	Mali	15.12272	2.08907	0	0
N3148	Boratynsky et a.,l 2017	tarabuli	Niger	15.01667	12.46667	0	0
N3324	Boratynsky et a.,l 2017	tarabuli	Niger	15.06666	10.70000	0	0
17927	Boratynsky et a.,l 2017	tarabuli	Libya	30.78000	17.83000	1	1
M5314	Boratynsky et a.,l 2017	tarabuli	Mali	19.01927	1.79913	1	1
M5929	Boratynsky et a.,l 2017	tarabuli	Mali	17.86307	-1.83068	1	1
M5930	Boratynsky et a.,l 2017	tarabuli	Mali	19.33048	-0.23362	1	1
M5932	Boratynsky et a.,l 2017	tarabuli	Mali	17.82325	-3.19743	1	1
M5945	Boratynsky et a.,l 2017	tarabuli	Mali	17.99783	0.46053	1	1
M5948	Boratynsky et a.,l 2017	tarabuli	Mali	19.78357	0.32807	1	1
M5949	Boratynsky et a.,l 2017	tarabuli	Mali	20.18763	0.97542	1	1
M5962	Boratynsky et a.,l 2017	Tarabuli	Mali	19.71160	0.18730	1	1
M5971	Boratynsky et a.,l 2017	Tarabuli	Mali	19.35568	-0.24178	1	1
M6134	Boratynsky et a.,l 2017	Tarabuli	Senegal	18.03032	0.47515	1	1
M6135	Boratynsky et a.,l 2017	Tarabuli	Senegal	19.41282	-0.57765	1	1
N3029	Boratynsky et a.,l 2017	Tarabuli	Niger	17.41667	6.78333	1	1
N3040	Boratynsky et a.,l 2017	Tarabuli	Niger	17.08333	7.45000	1	1
N3133	Boratynsky et a.,l 2017	Tarabuli	Niger	14.90000	12.51667	1	1
N3139	Boratynsky et a.,l 2017	Tarabuli	Niger	14.18333	13.18333	1	1
TAD8	Boratynsky et a.,l 2017	Tarabuli	Mali	17.37302	-2.80455	1	1

Table S2 Nearest Neighbor Index (NNI) results for all species after spatial filtering with a 5x5km grid.

Average Nearest Neighbor Summary												
Gerbillus:	*amoenus*	*campestris*	*gerbillus*	*henleyi*	*hesperinus*	*hoogstraali*	*nancillus*	*nigeriae*	*occiduus*	*pyramidum*	*sp*	*tarabuli*
Result:	clustered	clustered	clustered	random	dispersed	dispersed	clustered	random	random	clustered	clustered	clustered
Observed Mean Distance:	1.568196 Degrees	0.857028 Degrees	0.960828 Degrees	2.144186 Degrees	0.055384 Degrees	0.158146 Degrees	0.626665 Degrees	1.618657 Degrees	0.256195 Degrees	1.068904 Degrees	0.017065 Degrees	0.816532 Degrees
Expected Mean Distance:	2.310768 Degrees	1.364920 Degrees	1.581177 Degrees	2.553336 Degrees	0.035232 Degrees	0.110774 Degrees	0.859881 Degrees	1.486590 Degrees	0.332071 Degrees	2.057578 Degrees	0.077267 Degrees	1.482066 Degrees
Nearest Neighbor Ratio:	0.678646	0.627897	0.607666	0.839759	1.572014	1.427642	0.728781	1.088839	0.771507	0.519496	0.220076	0.550921
z-score:	-4.390353	-7.294393	-7.199139	-1.33623	3.945565	3.272439	-2.201342	0.797161	-1.635568	-7.635762	-4.94857	-7.440186
p-value:	0.00011	0.00010	-0.00002	0.181473	0.00008	0.001066	0.027712	0.425358	0.10193	0.00150	0.000044	0.00012

Table S3 Correlation matrix of climatic variables. Highlighted in red are the strong correlations (R>70). Highlighted in bold the selected variables.

Layer	Bio1	**Bio2**	Bio3	Bio4	**Bio5**	**Bio6**	**Bio7**	Bio8	Bio9	Bio10	Bio11	Bio12	Bio13	Bio14	Bio15	**Bio16**	Bio17	Bio18	**Bio19**
Bio1	1	0.37511	0.59387	-0.445	0.69172	0.84585	-0.2265	0.83651	0.04178	0.79806	0.90897	0.0696	0.31028	-0.5596	0.65614	0.25875	-0.6011	0.31165	-0.5449
Bio2	0.37511	1	0.16605	0.22023	0.65601	-0.0533	0.54548	0.32543	-0.0884	0.52171	0.14525	-0.3182	-0.1688	-0.3103	0.10847	-0.2075	-0.3979	-0.1557	-0.4847
Bio3	0.59387	0.16605	1	-0.907	-0.0357	0.7839	-0.7238	0.49553	-0.2086	0.03489	0.82333	0.39415	0.59913	-0.3439	0.66097	0.54937	-0.3974	0.53144	-0.3124
Bio4	-0.445	0.22023	-0.907	1	0.27323	-0.8001	0.91859	-0.3646	0.15456	0.16582	-0.7714	-0.5923	-0.7301	0.18077	-0.6342	-0.6969	0.1957	-0.6326	0.08251
Bio5	0.69172	0.65601	-0.0357	0.27323	1	0.27152	0.51799	0.56864	0.24824	0.96209	0.3769	-0.2412	-0.1042	-0.3592	0.22097	-0.132	-0.3962	-0.0617	-0.4702
Bio6	0.84585	-0.0533	0.7839	-0.8001	0.27152	1	-0.6826	0.71468	0.00954	0.41495	0.97222	0.37537	0.56668	-0.3926	0.73338	0.52532	-0.4049	0.53062	-0.3036
Bio7	-0.2265	0.54548	-0.7238	0.91859	0.51799	-0.6826	1	-0.2034	0.18001	0.36174	-0.5779	-0.5168	-0.5828	0.07618	-0.484	-0.5671	0.05903	-0.5185	-0.0872
Bio8	0.83651	0.32543	0.49553	-0.3646	0.56864	0.71468	-0.2034	1	-0.1922	0.65094	0.74969	-0.0438	0.1413	-0.3681	0.63739	0.0962	-0.4158	0.23088	-0.4545
Bio9	0.04178	-0.0884	-0.2086	0.15456	0.24824	0.00954	0.18001	-0.1922	1	0.22503	-0.009	0.14042	0.12479	-0.0157	0.06949	0.13315	0.0321	0.07586	0.0724
Bio10	0.79806	0.52171	0.03489	0.16582	0.96209	0.41495	0.36174	0.65094	0.22503	1	0.49794	-0.2309	-0.068	-0.4606	0.29276	-0.0992	-0.489	-0.0216	-0.5101
Bio11	0.90897	0.14525	0.82333	-0.7714	0.3769	0.97222	-0.5779	0.74969	-0.009	0.49794	1	0.36254	0.58774	-0.4582	0.74758	0.53879	-0.4906	0.53741	-0.4039
Bio12	0.0696	-0.3182	0.39415	-0.5923	-0.2412	0.37537	-0.5168	-0.0438	0.14042	-0.2309	0.36254	1	0.94366	0.24333	0.2521	0.96683	0.28341	0.77085	0.35735
Bio13	0.31028	-0.1688	0.59913	-0.7301	-0.1042	0.56668	-0.5828	0.1413	0.12479	-0.068	0.58774	0.94366	1	0.01696	0.43125	0.99373	0.02804	0.8177	0.10356
Bio14	-0.5596	-0.3103	-0.3439	0.18077	-0.3592	-0.3926	0.07618	-0.3681	-0.0157	-0.4606	-0.4582	0.24333	0.01696	1	-0.2556	0.05125	0.95966	0.10158	0.52004
Bio15	0.65614	0.10847	0.66097	-0.6342	0.22097	0.73338	-0.484	0.63739	0.06949	0.29276	0.74758	0.2521	0.43125	-0.2556	1	0.3734	-0.2854	0.40929	-0.1984
Bio16	0.25875	-0.2075	0.54937	-0.6969	-0.132	0.52532	-0.5671	0.0962	0.13315	-0.0992	0.53879	0.96683	0.99373	0.05125	0.3734	1	0.06967	0.81185	0.15618
Bio17	-0.6011	-0.3979	-0.3974	0.1957	-0.3962	-0.4049	0.05903	-0.4158	0.0321	-0.489	-0.4906	0.28341	0.02804	0.95966	-0.2854	0.06967	1	0.09905	0.63067
Bio18	0.31165	-0.1557	0.53144	-0.6326	-0.0617	0.53062	-0.5185	0.23088	0.07586	-0.0216	0.53741	0.77085	0.8177	0.10158	0.40929	0.81185	0.09905	1	0.02872
Bio19	-0.5449	-0.4847	-0.3124	0.08251	-0.4702	-0.3036	-0.0872	-0.4545	0.0724	-0.5101	-0.4039	0.35735	0.10356	0.52004	-0.1984	0.15618	0.63067	0.02872	1

Table S4 Percentages of suitable pixels of species allocated to each ecoregion group. Highlighted the higher percentages for each species.

	Saharan	Sahelian	Mediterranean	Mountains	Atlantic Sahara
G.amoenus	**63.62%**	21.69%	9.60%	4.62%	0.48%
G.campestris	**56.18%**	25.11%	12.87%	5.28%	0.55%
G.gerbillus	**77.24%**	13.40%	5.04%	3.90%	0.42%
G.henleyi	2.94%	**70.92%**	25.73%	0.23%	0.18%
G.hesperinus	0.00%	0.00%	**100.00%**	0.00%	0.00%
G.hoogstraali	16.64%	1.64%	**79.23%**	0.00%	2.49%
G.nancillus	0.01%	**99.99%**	0.00%	0.00%	0.00%
G.nigeriae	10.23%	**84.17%**	3.93%	0.12%	1.55%
G.occiduus	**41.75%**	0.00%	**26.84%**	0.00%	**31.41%**
G.sp	19.20%	0.00%	**70.63%**	0.00%	10.17%
G.pyramidum	**68.48%**	18.63%	8.42%	4.04%	0.42%
G.tarabuli	**62.81%**	29.73%	4.22%	2.82%	0.42%

Table S5 Percentages of pixels of ecoregion groups that are considered suitable for each species. Highlighted the higher percentages for each species.

	Saharan	Sahelian	Mediterranean	Mountains	Atlantic Sahara
G. amoenus	**64.93%**	**53.49%**	**87.71%**	**98.33%**	**94.09%**
G. campestris	**48.70%**	**52.49%**	**99.68%**	**95.33%**	**91.12%**
G. gerbillus	**90.67%**	38.09%	**53.13%**	**95.82%**	**94.09%**
G. henleyi	1.24%	**68.83%**	**92.55%**	1.94%	13.85%
G. hesperinus	0.00%	0.00%	0.09%	0.00%	0.00%
G. hoogstraali	1.03%	0.22%	38.54%	0.00%	25.86%
G. nancillus	0.00%	**45.07%**	0.00%	0.00%	0.00%
G. nigeriae	3.70%	**64.43%**	11.15%	0.82%	**94.09%**
G. occiduus	0.42%	0.00%	1.37%	0.00%	34.39%
Gerbillus sp.	0.09%	0.00%	2.00%	0.00%	6.15%
G. pyramidum	**78.83%**	**51.89%**	**86.93%**	**97.16%**	**93.50%**
G. tarabuli	**72.96%**	**83.51%**	**43.88%**	**68.42%**	**94.09%**

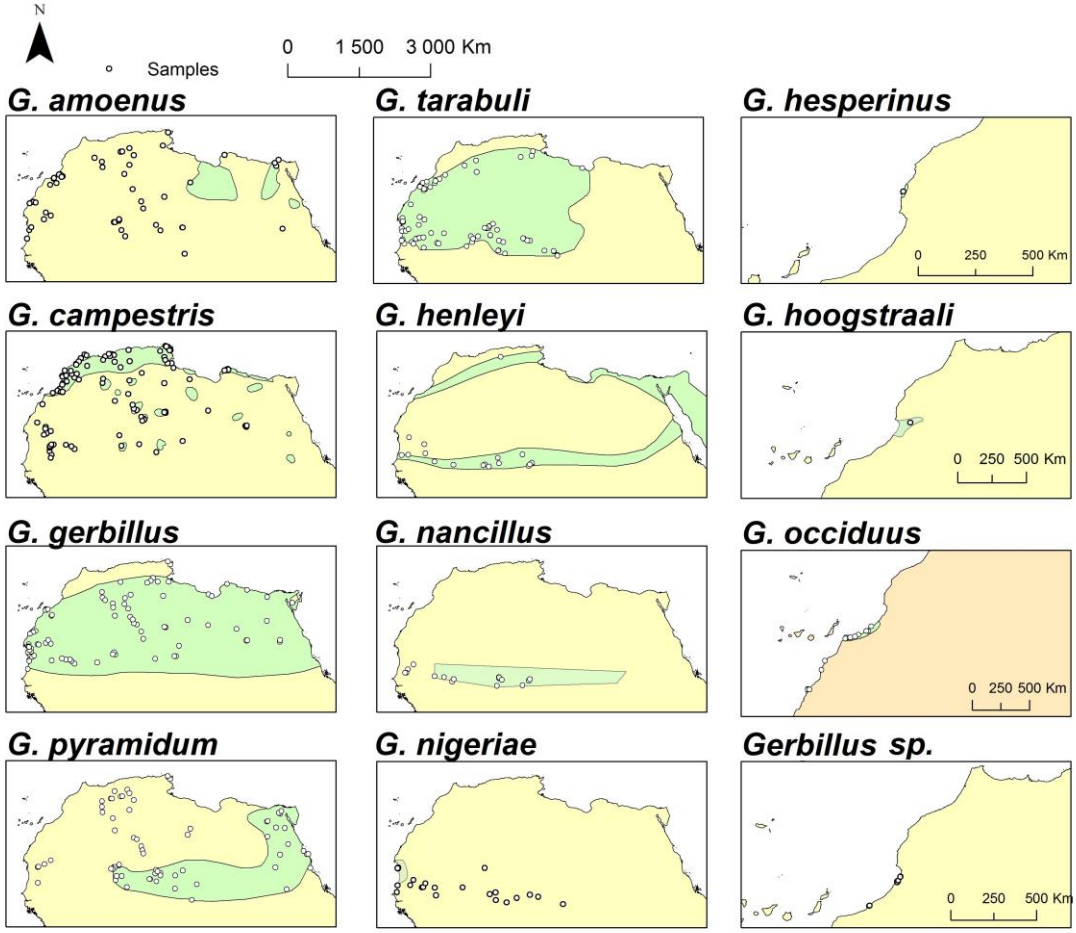

Fig. S1 Species described distributions of IUCN (in green) and corresponding observations used in this study. *Gerbillus sp.* does not have a described distribution in IUCN. The maps of the right have been zoomed independently and have a corresponding scale bar.

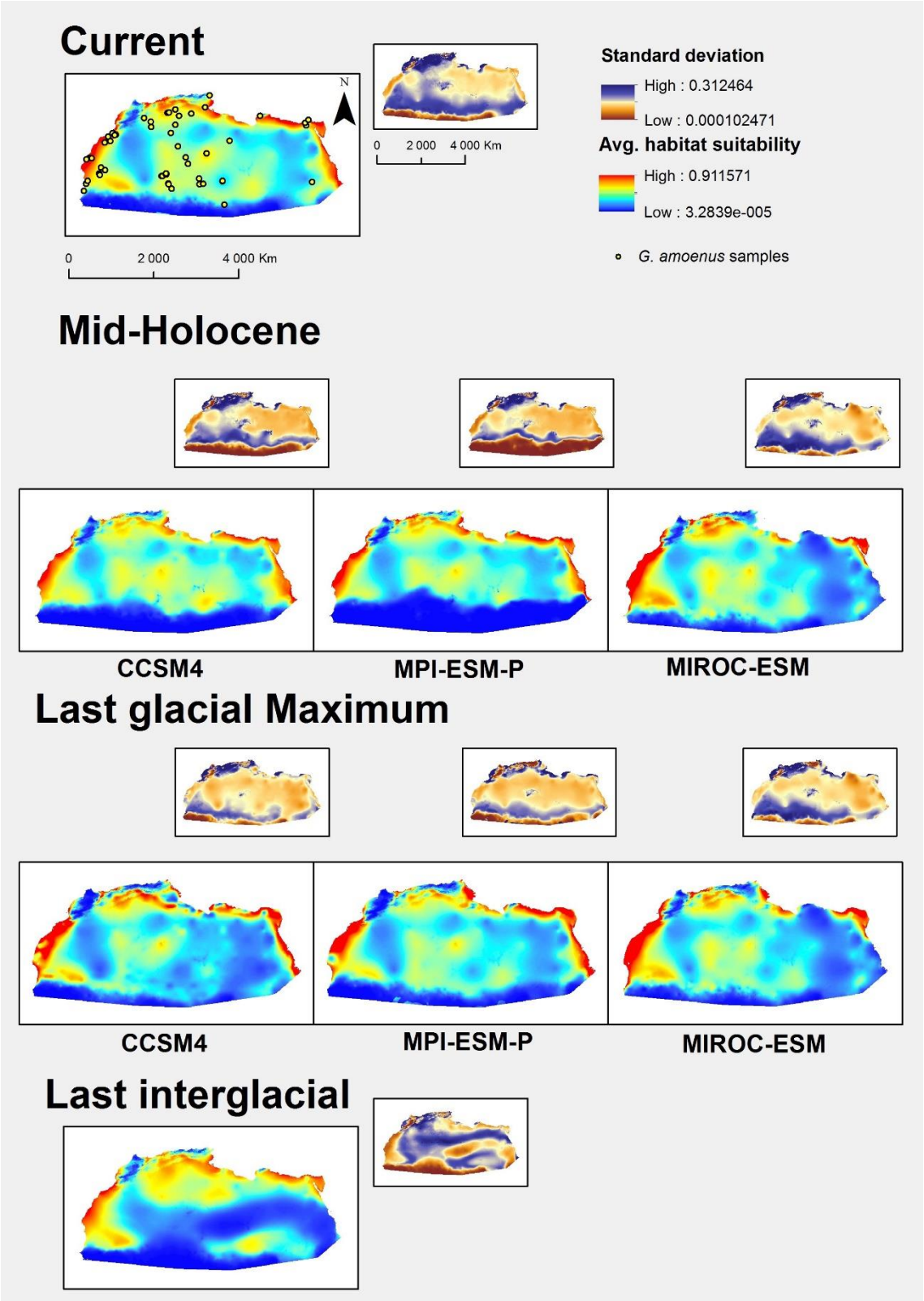

Fig. S2 Climatic models and projections to the past of *G. amoenus*, with corresponding standard deviations.

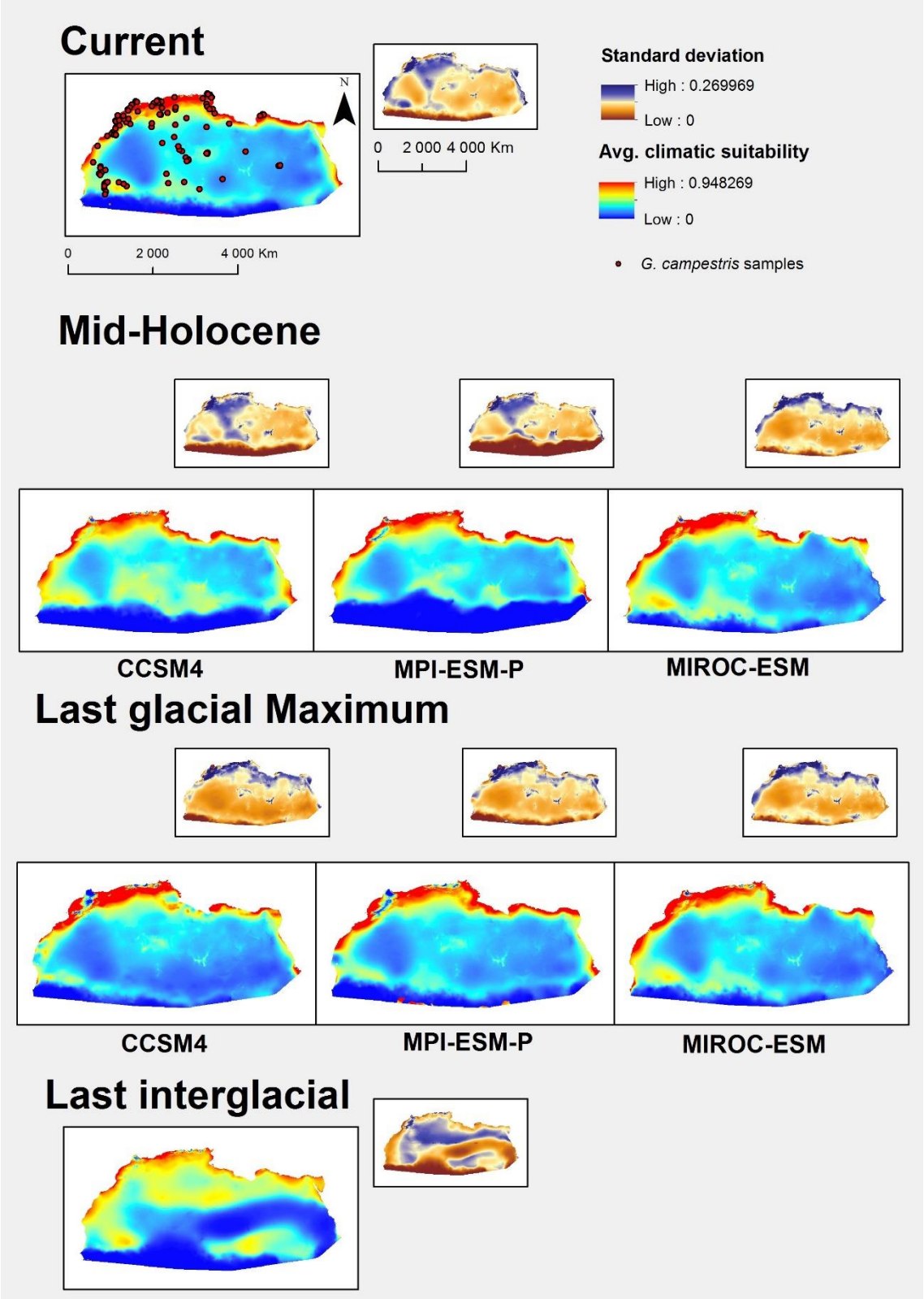

Fig. S3 Climatic models and projections to the past of *G. campestris*, with corresponding standard deviations.

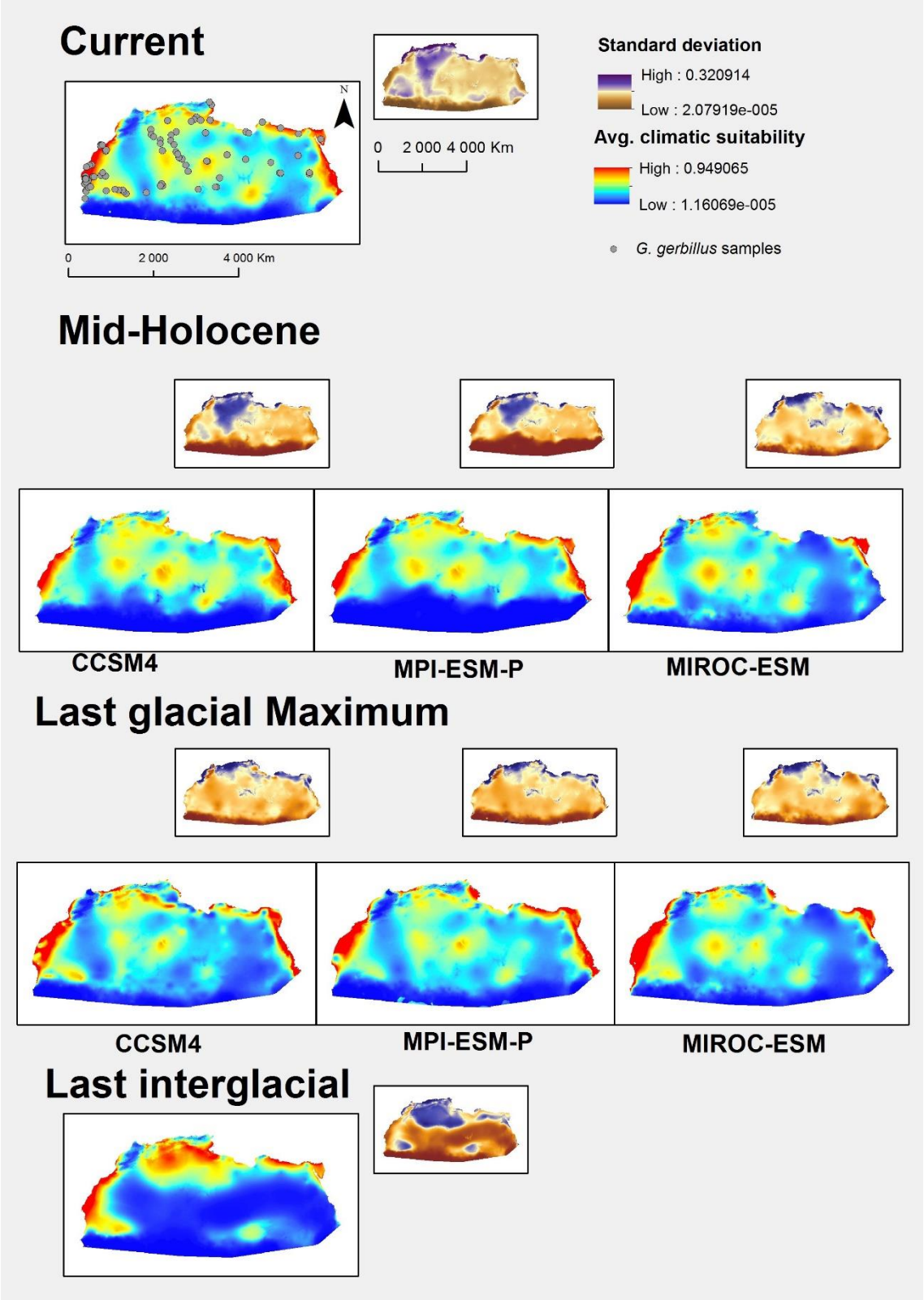

Fig. S4 Climatic models and projections to the past of *G. gerbillus*, with corresponding standard deviations.

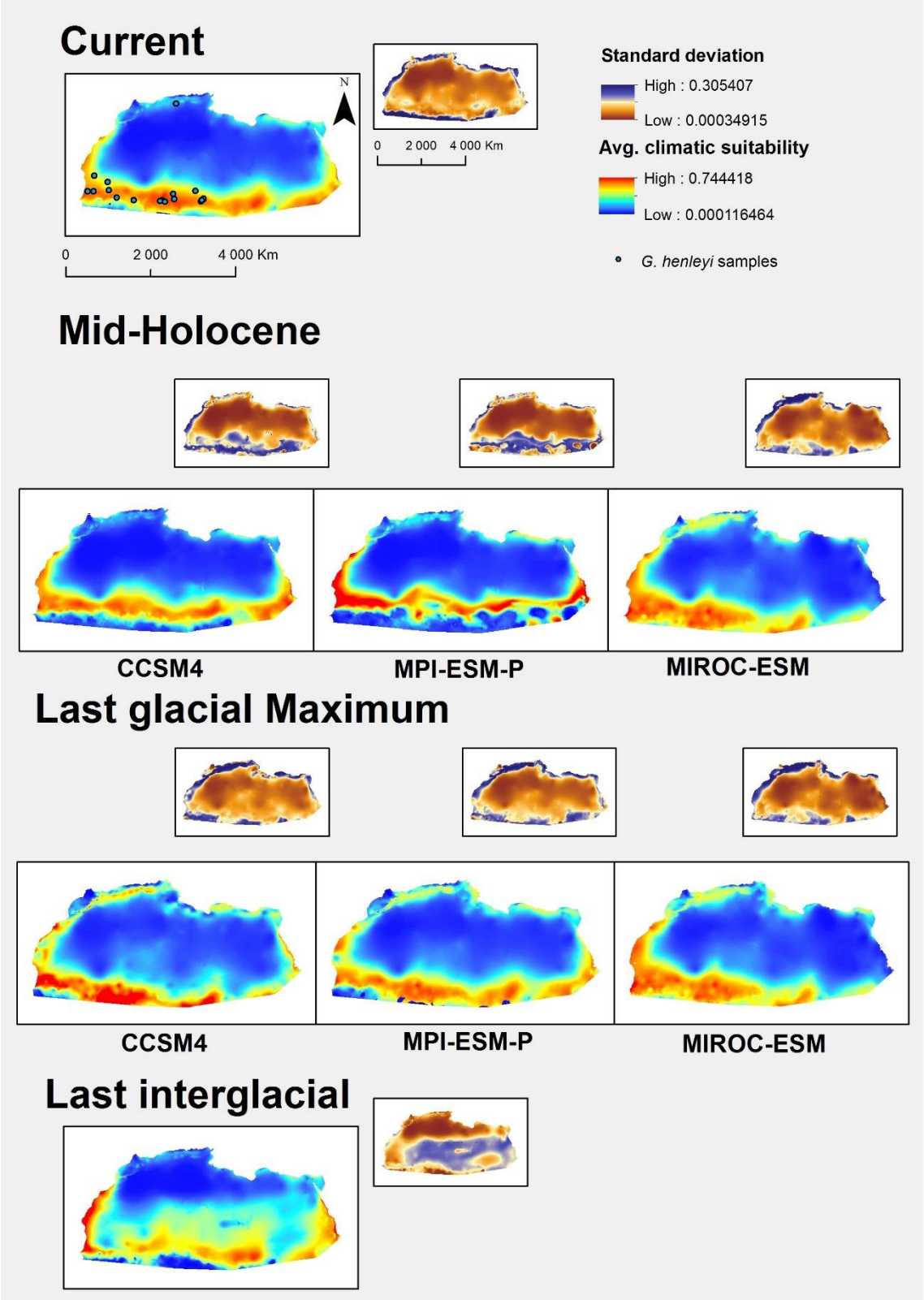

Fig. S5 Climatic models and projections to the past of *G. henleyi*, with corresponding standard deviations.

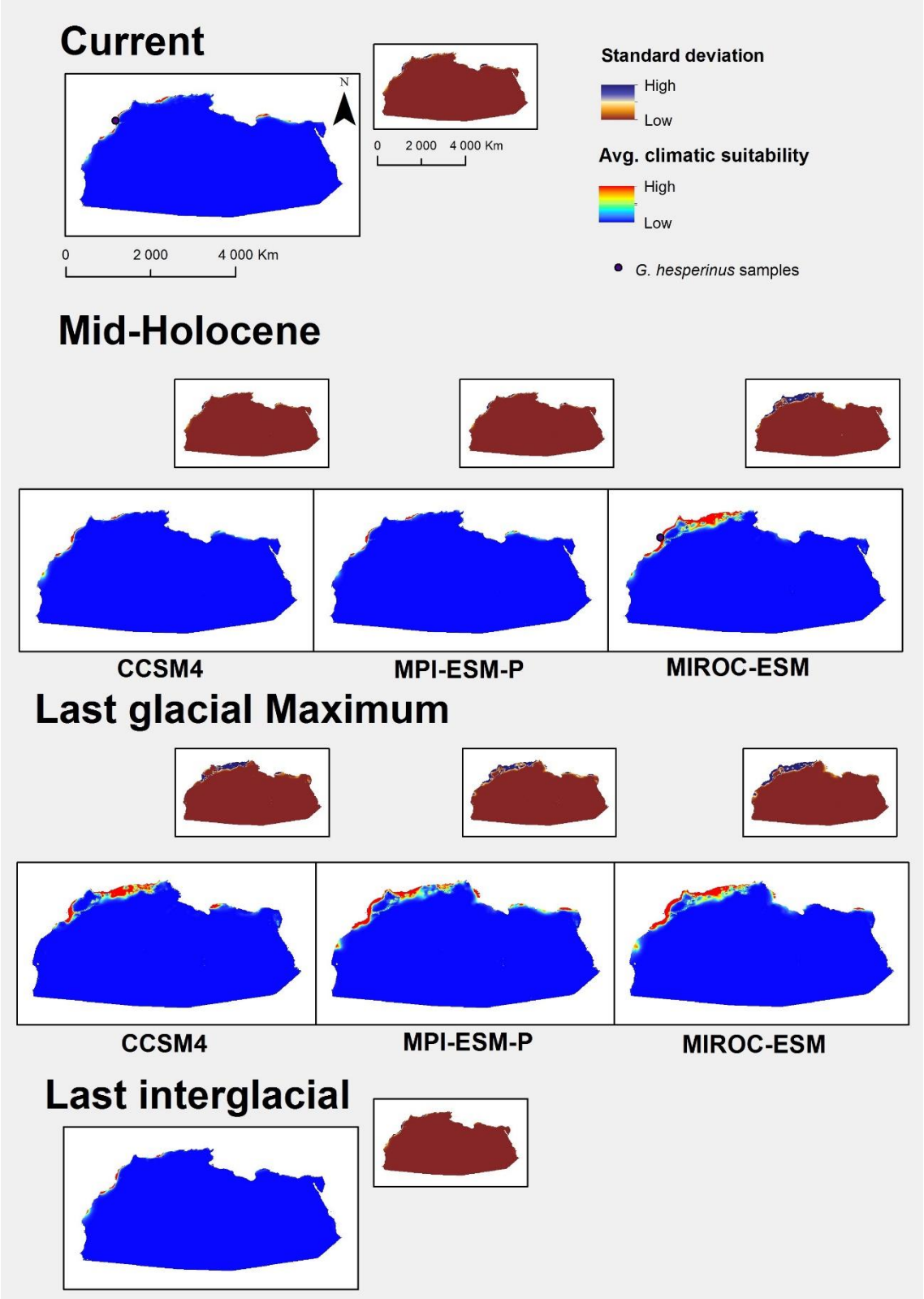

Fig. S6 Climatic models and projections to the past of *G. hesperinus*, with corresponding standard deviations.

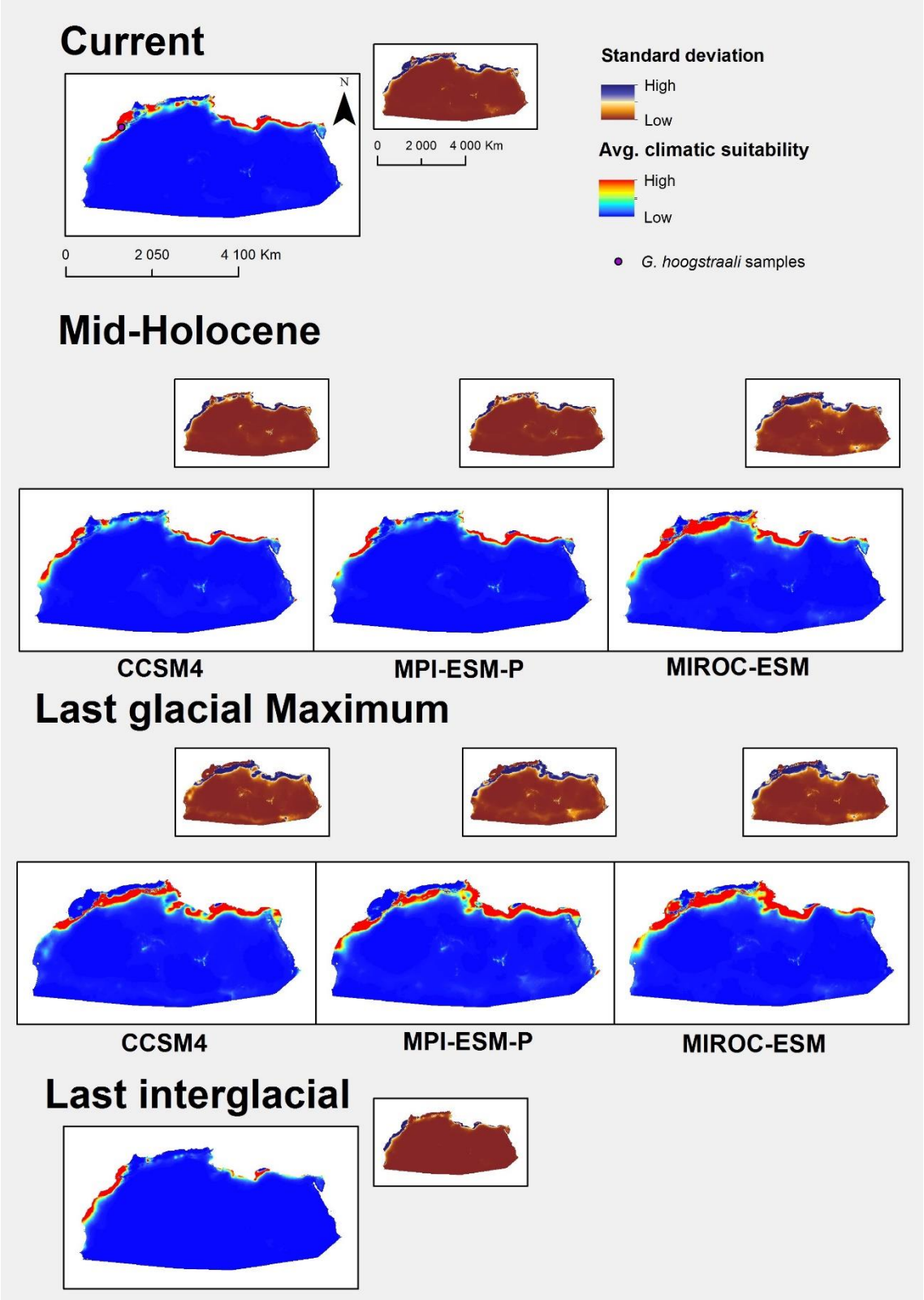

Fig. S7 Climatic models and projections to the past of *G. hoogstraali*, with corresponding standard deviations.

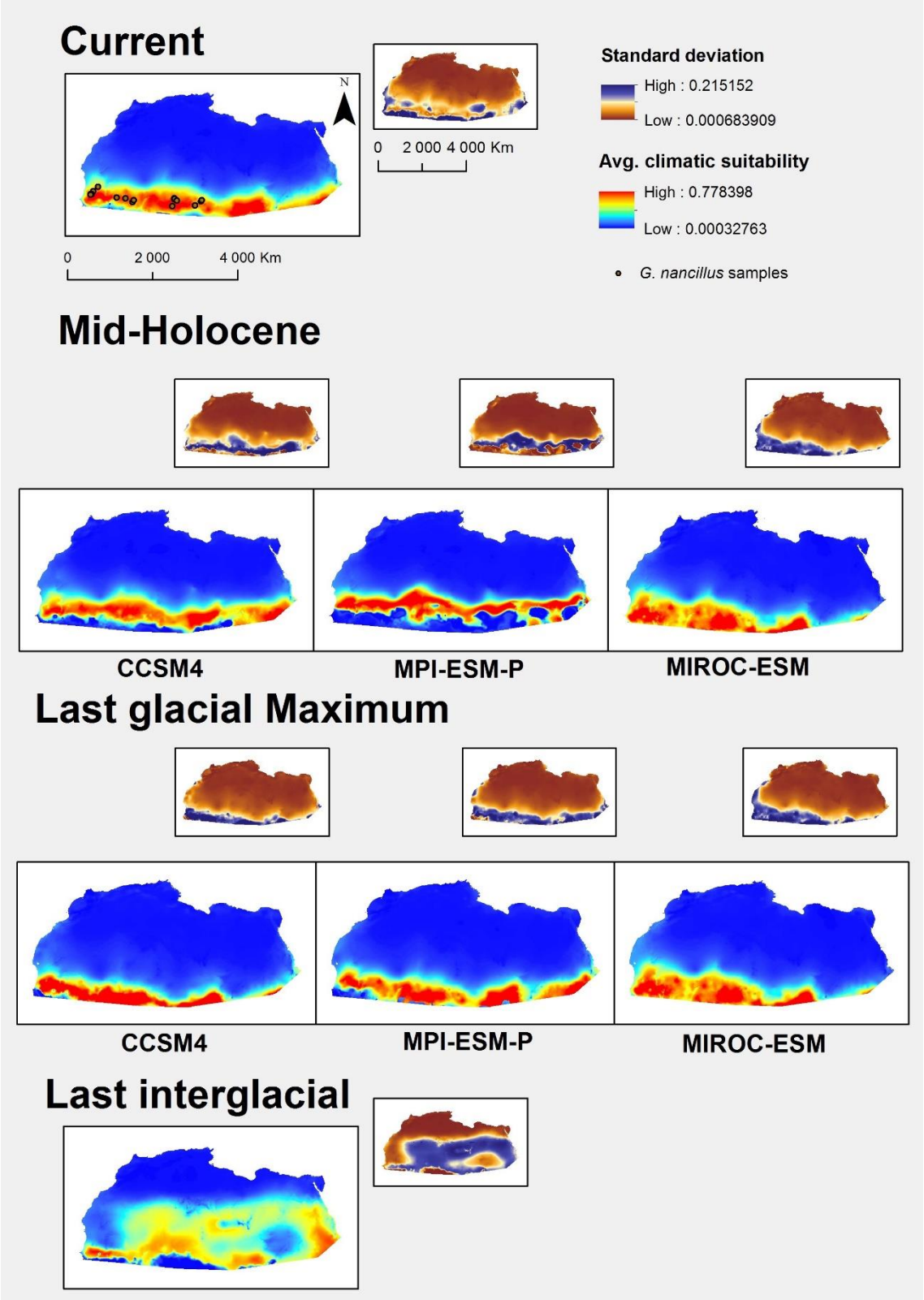

Fig. S8 Climatic models and projections to the past of *G. nancillus*, with corresponding standard deviations.

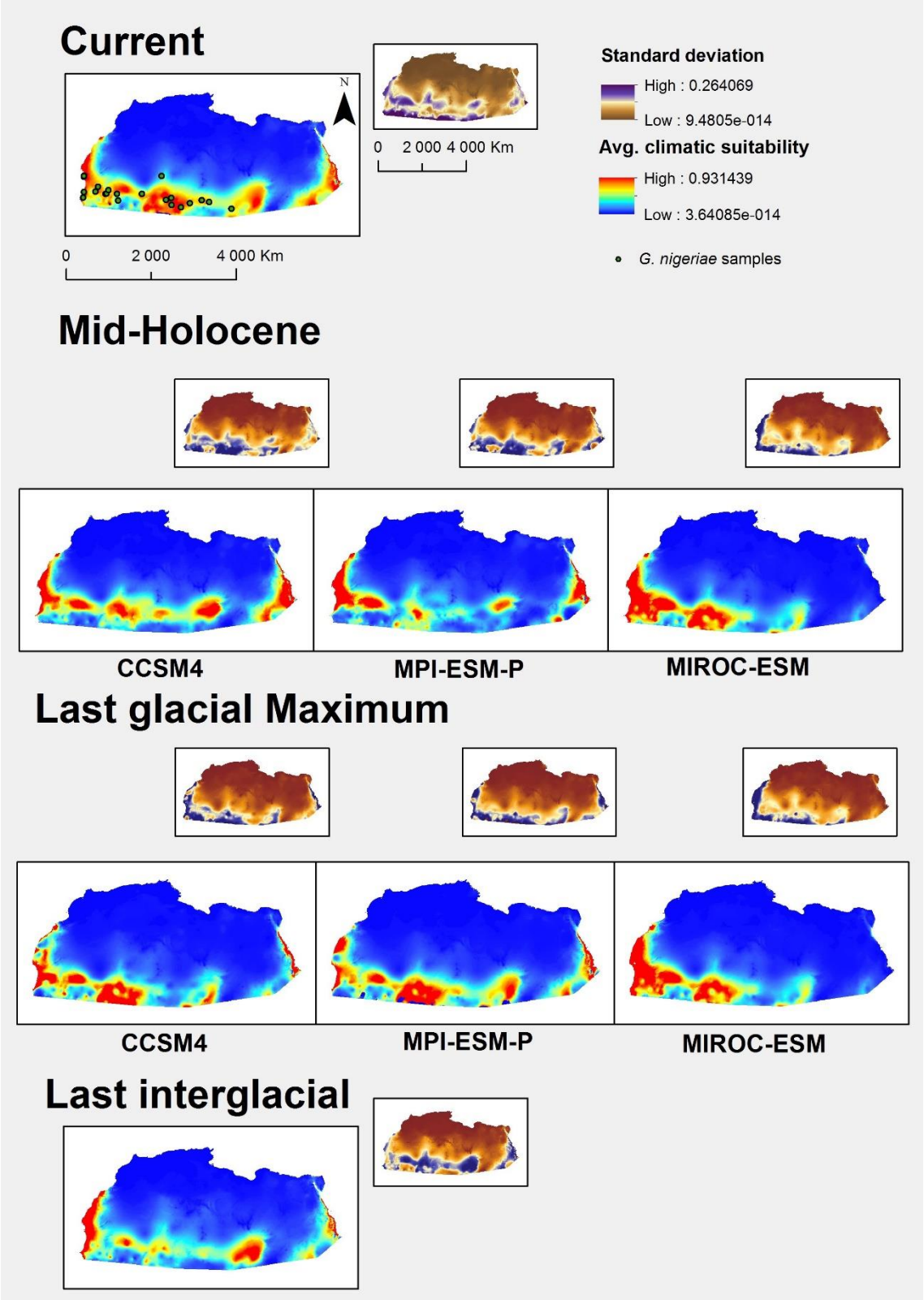

Fig. S9 Climatic models and projections to the past of *G. nigeriae*, with corresponding standard deviations.

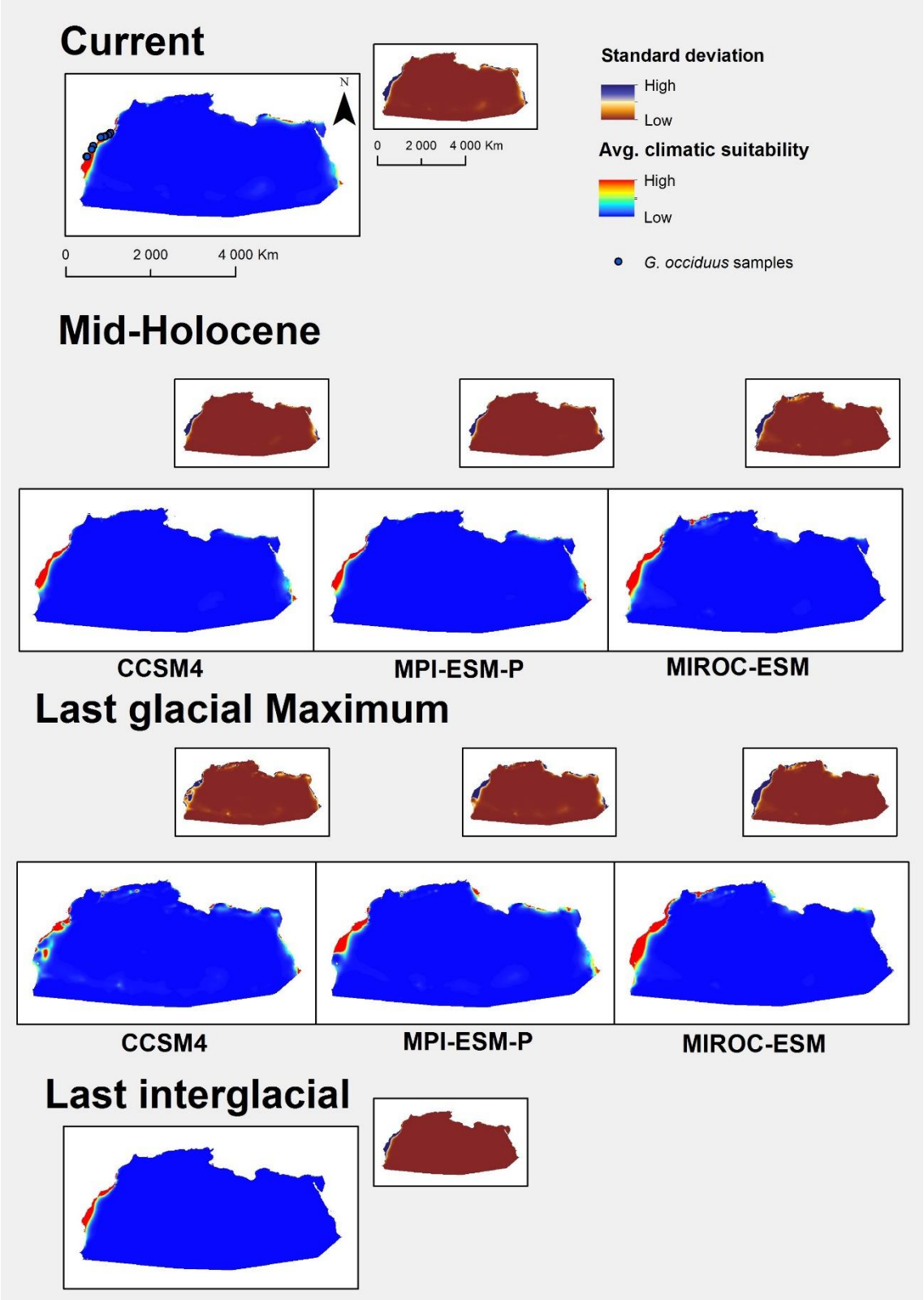

Fig. S10 Climatic models and projections to the past of *G. occiduus*, with corresponding standard deviations.

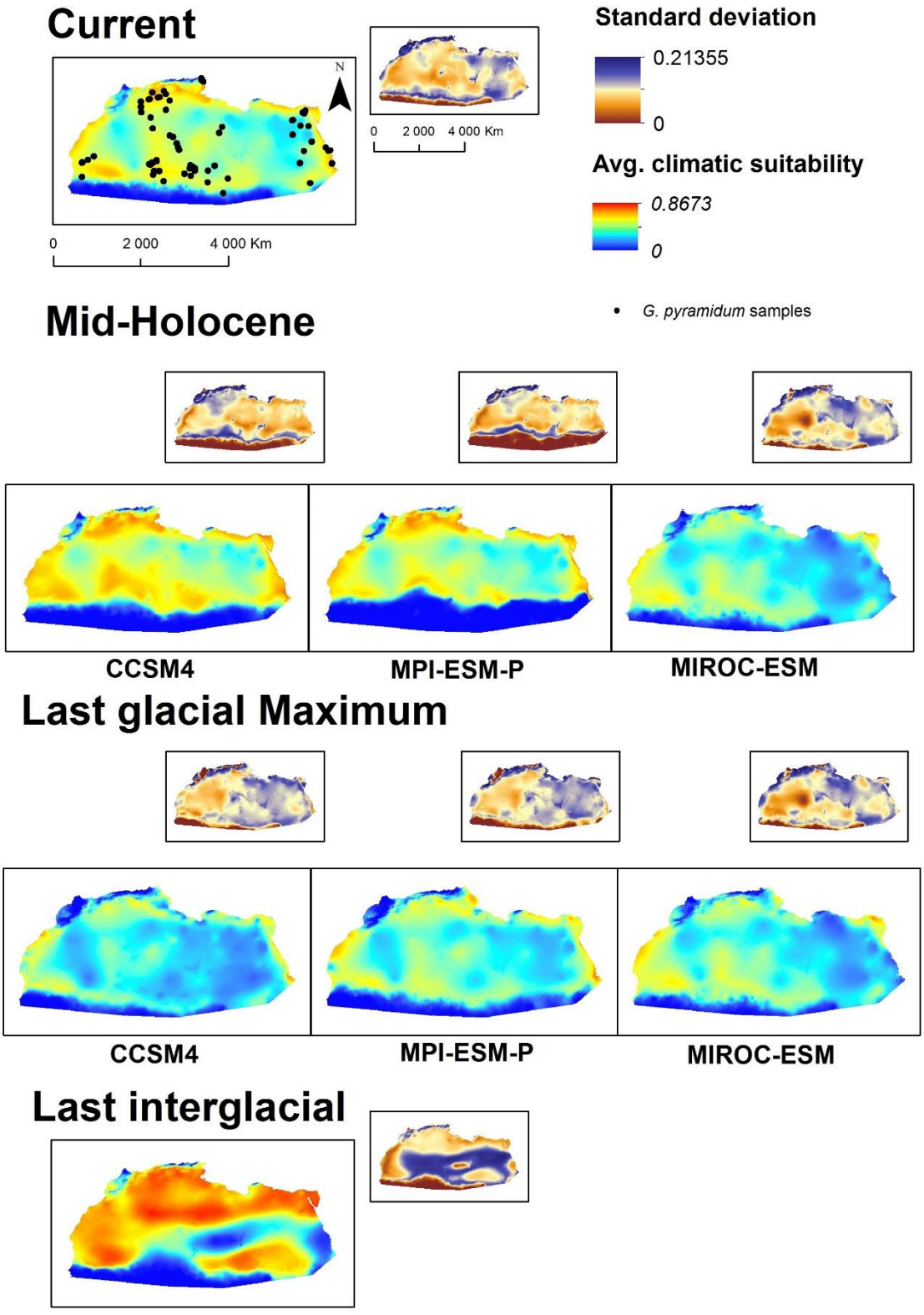

Fig. S11 Climatic models and projections to the past of *G. pyramidum*, with corresponding standard deviations.

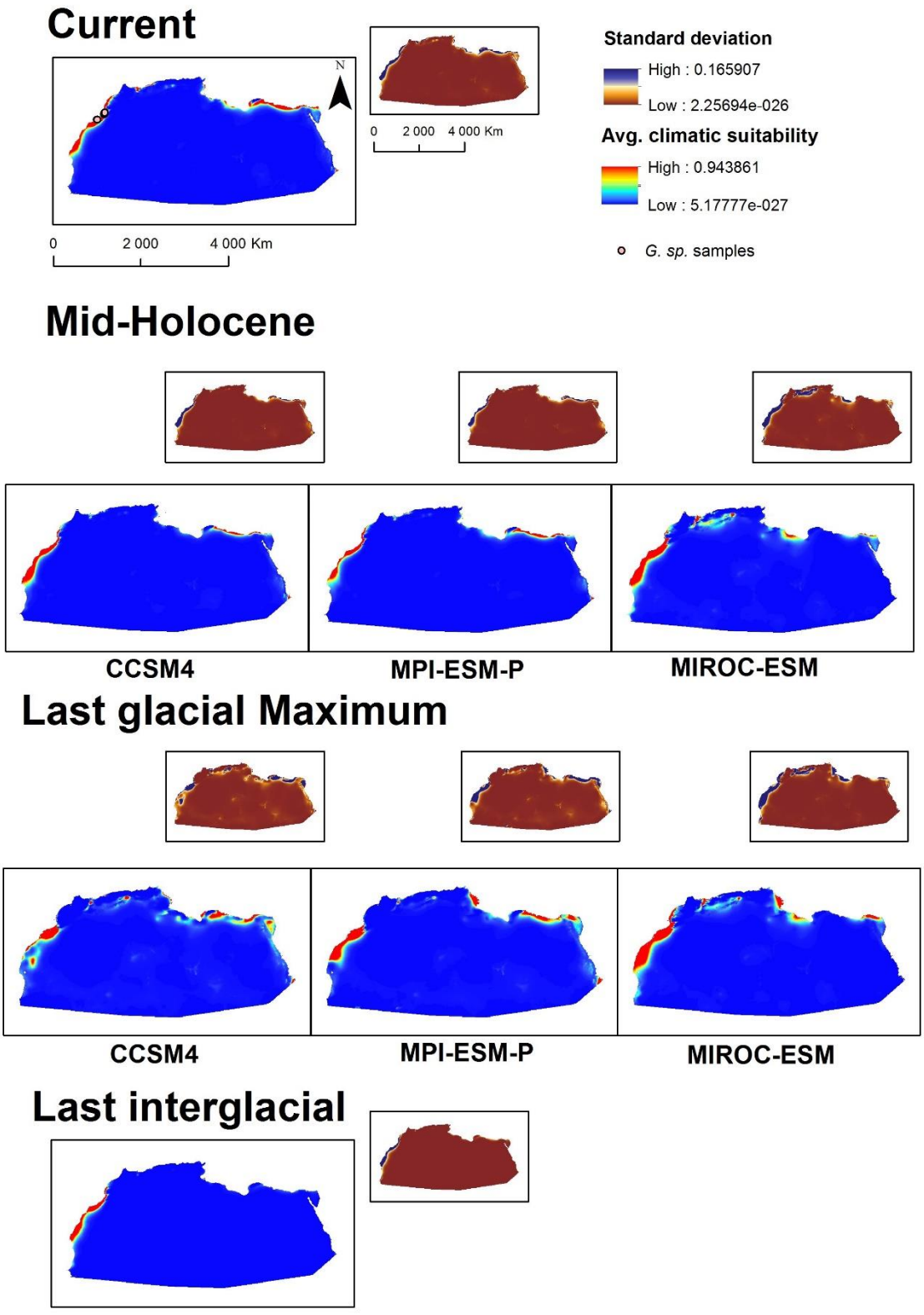

Fig. S12 Climatic models and projections to the past of *Gerbillus sp.*, with corresponding standard deviations.

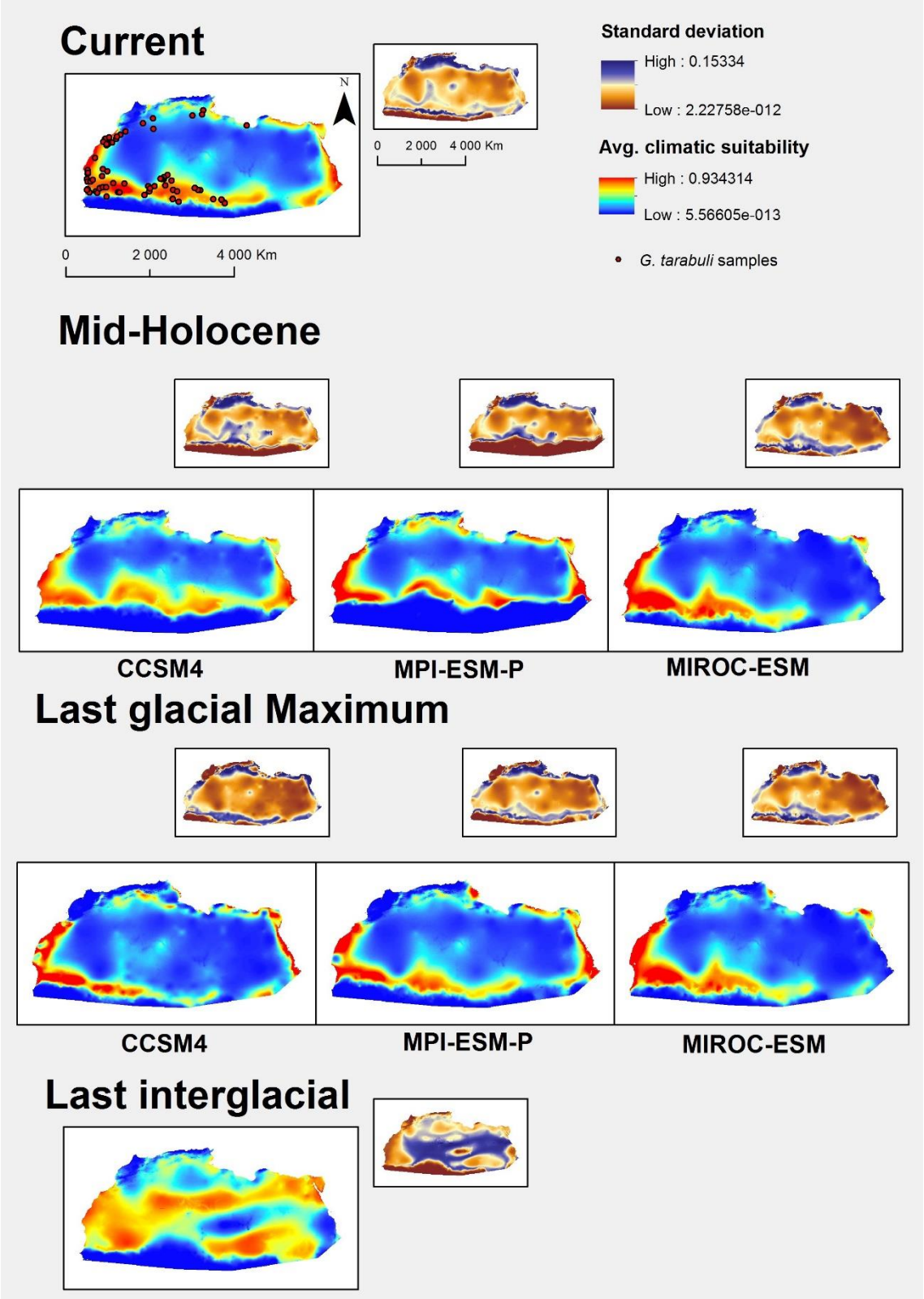

Fig. S13 Climatic models and projections to the past of *G. tarabuli*, with corresponding standard deviations.

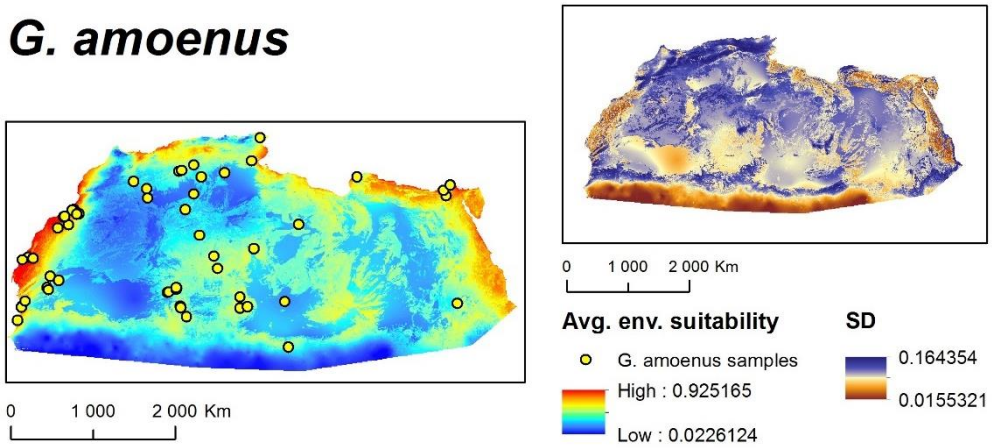

Fig. S14 Model of *G. amoenus* for current topo-climatic and landcover variables (at the left), with corresponding standard deviation (at the right).

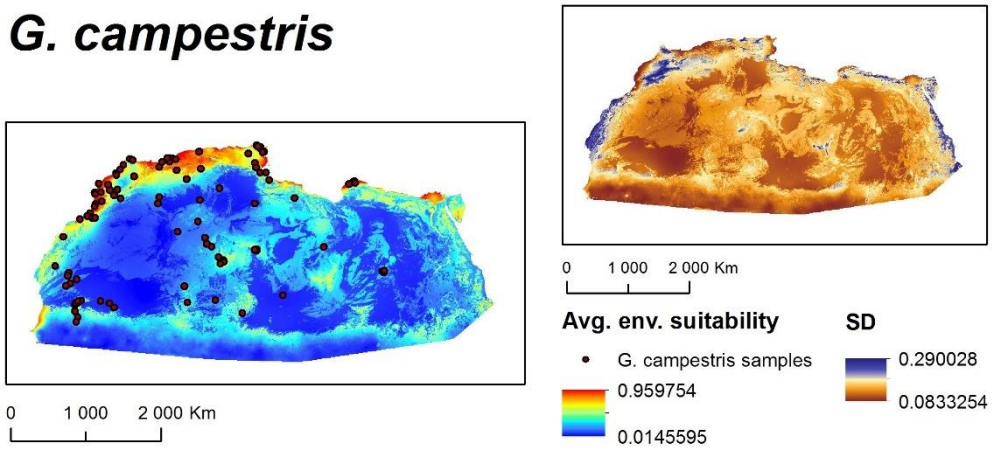

Fig. S15 Model of *G. campestris* for current topo-climatic and landcover variables (at the left), with corresponding standard deviation (at the right).

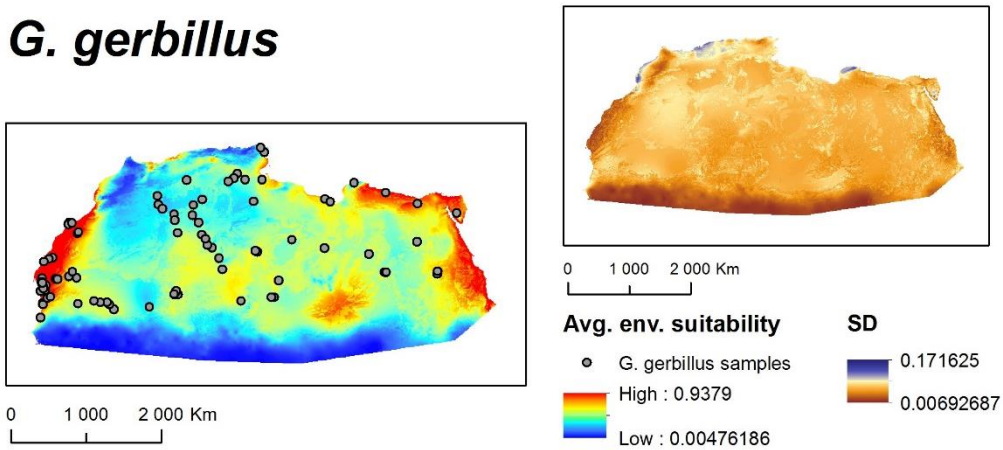

Fig. S16 Model of G. gerbillus for current topo-climatic and landcover variables (at the left), with corresponding standard deviation (at the right)

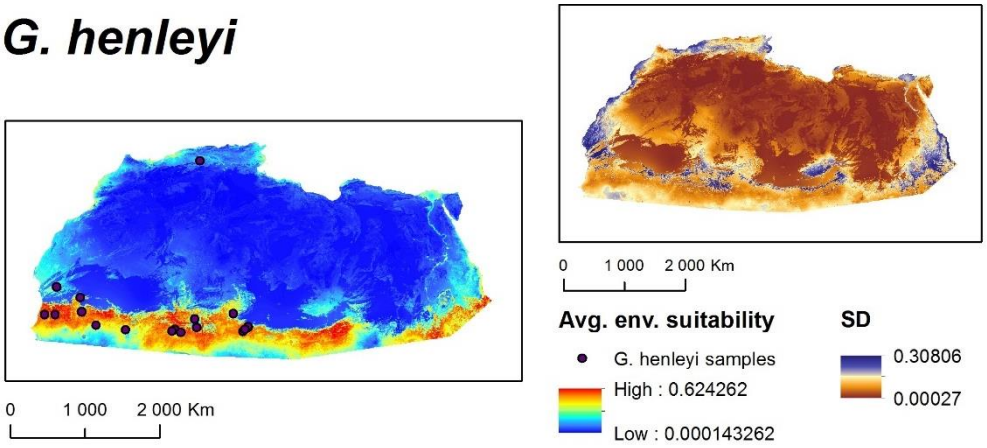

Fig. S17 Model of G. *henleyi* for current topo-climatic and landcover variables (at the left), with corresponding standard deviation (at the right)

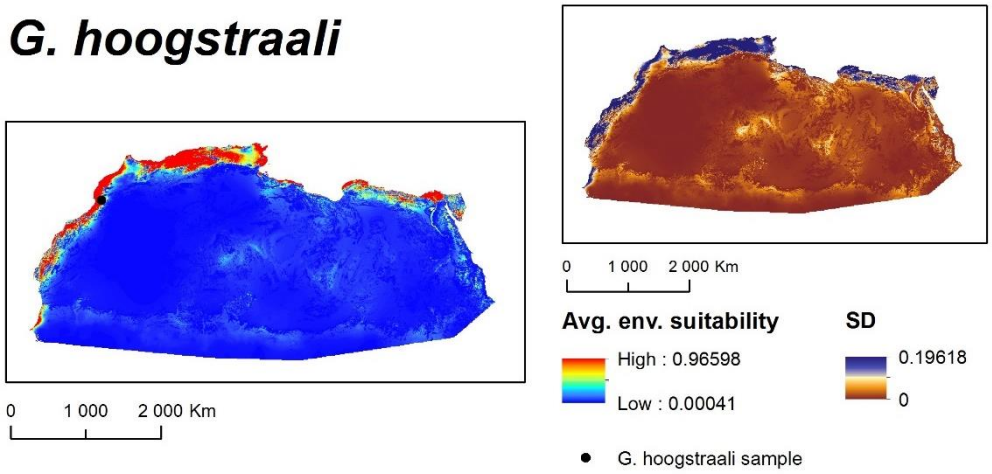

Fig. S18 Model of G. *hoogstraali* for current topo-climatic and landcover variables (at the left), with corresponding standard deviation (at the right)

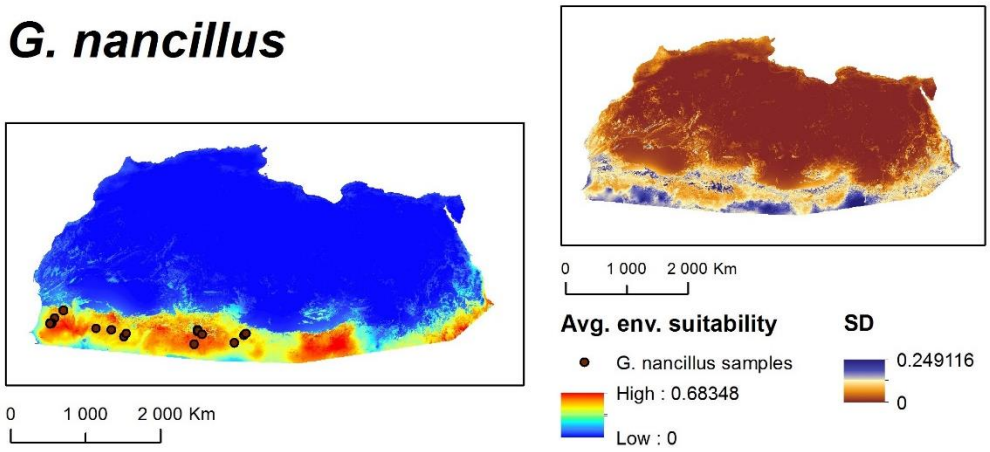

Fig. S19 Model of G. *nancillus* for current topo-climatic and landcover variables (at the left), with corresponding standard deviation (at the right)

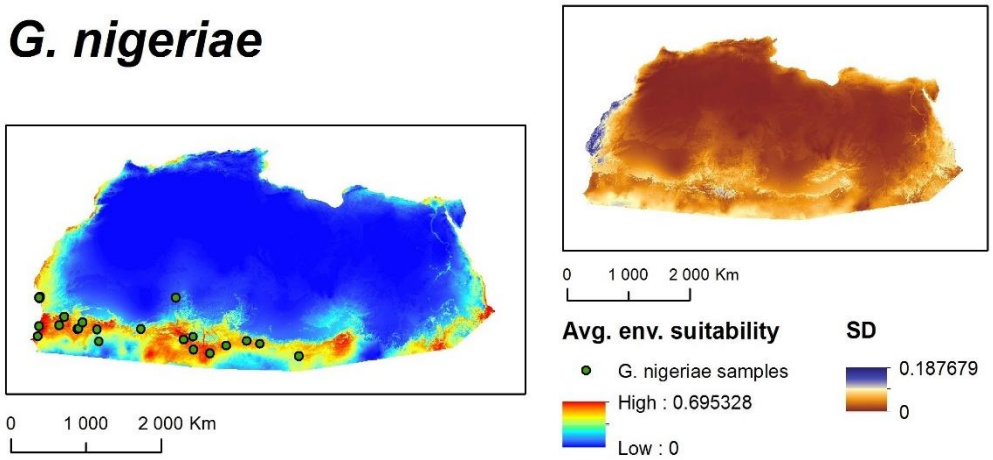

Fig. S20 Model of G. *nigeriae* for current topo-climatic and landcover variables (at the left), with corresponding standard deviation (at the right).

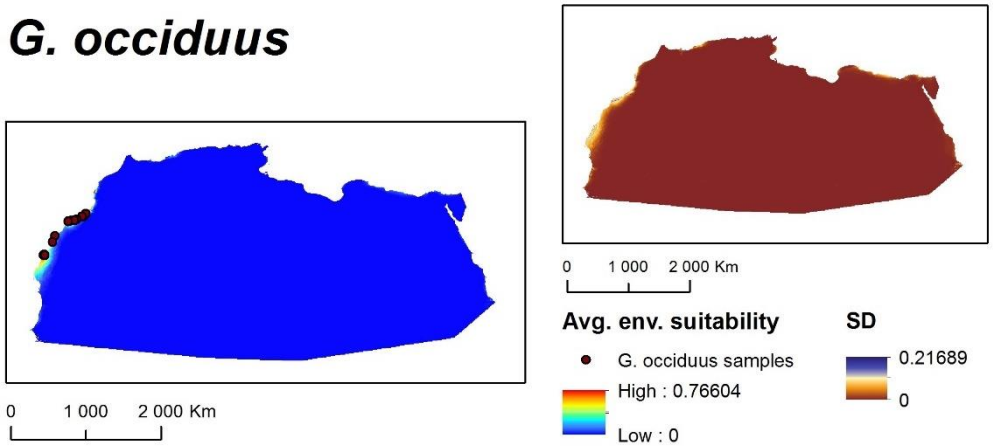

Fig. S21 Model of G. *occiduus* for current topo-climatic and landcover variables (at the left), with corresponding standard deviation (at the right).

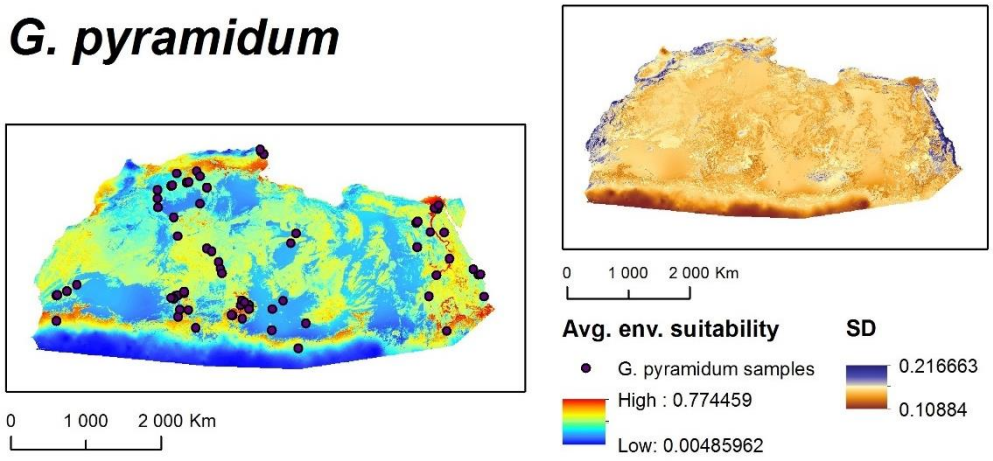

Fig. S22 Model of G. *pyramidum* for current topo-climatic and landcover variables (at the left), with corresponding standard deviation (at the right).

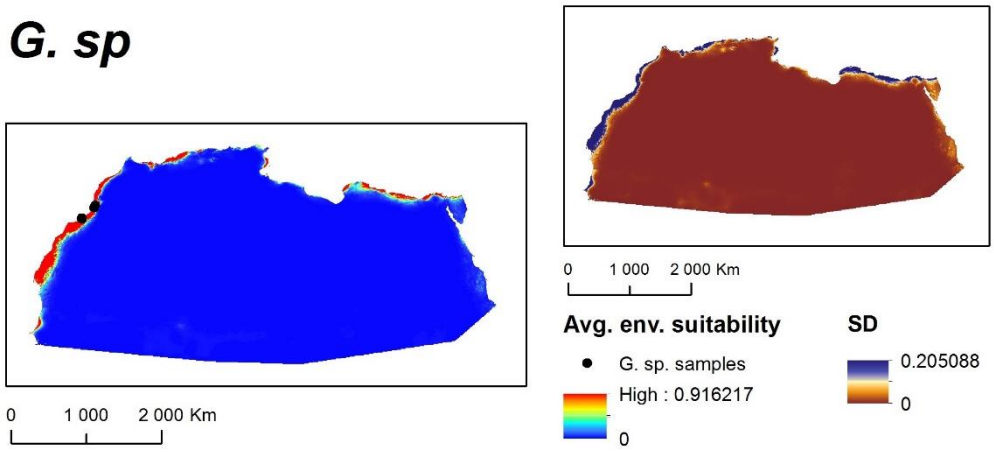

Fig. S23 Model of Gerbillus sp. for current topo-climatic and landcover variables (at the left), with corresponding standard deviation (at the right).

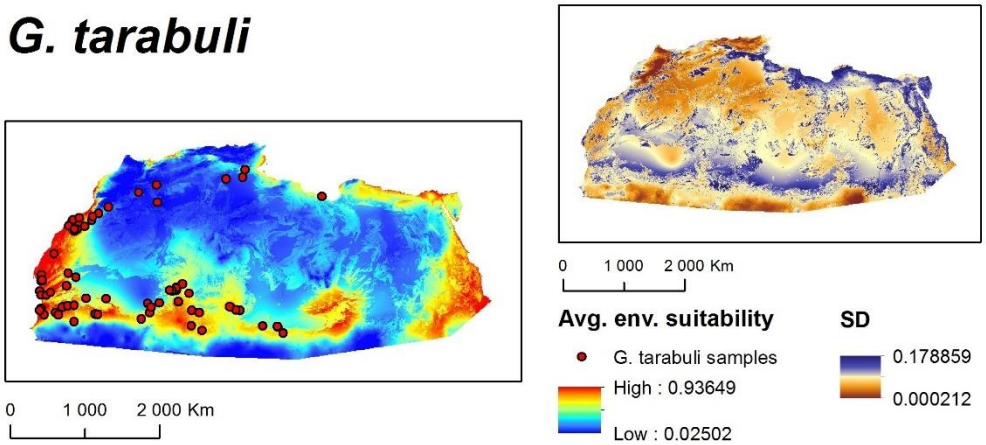

Fig. S24 Model of G. *tarabuli* for current topo-climatic and landcover variables (at the left), with corresponding standard deviation (at the right).

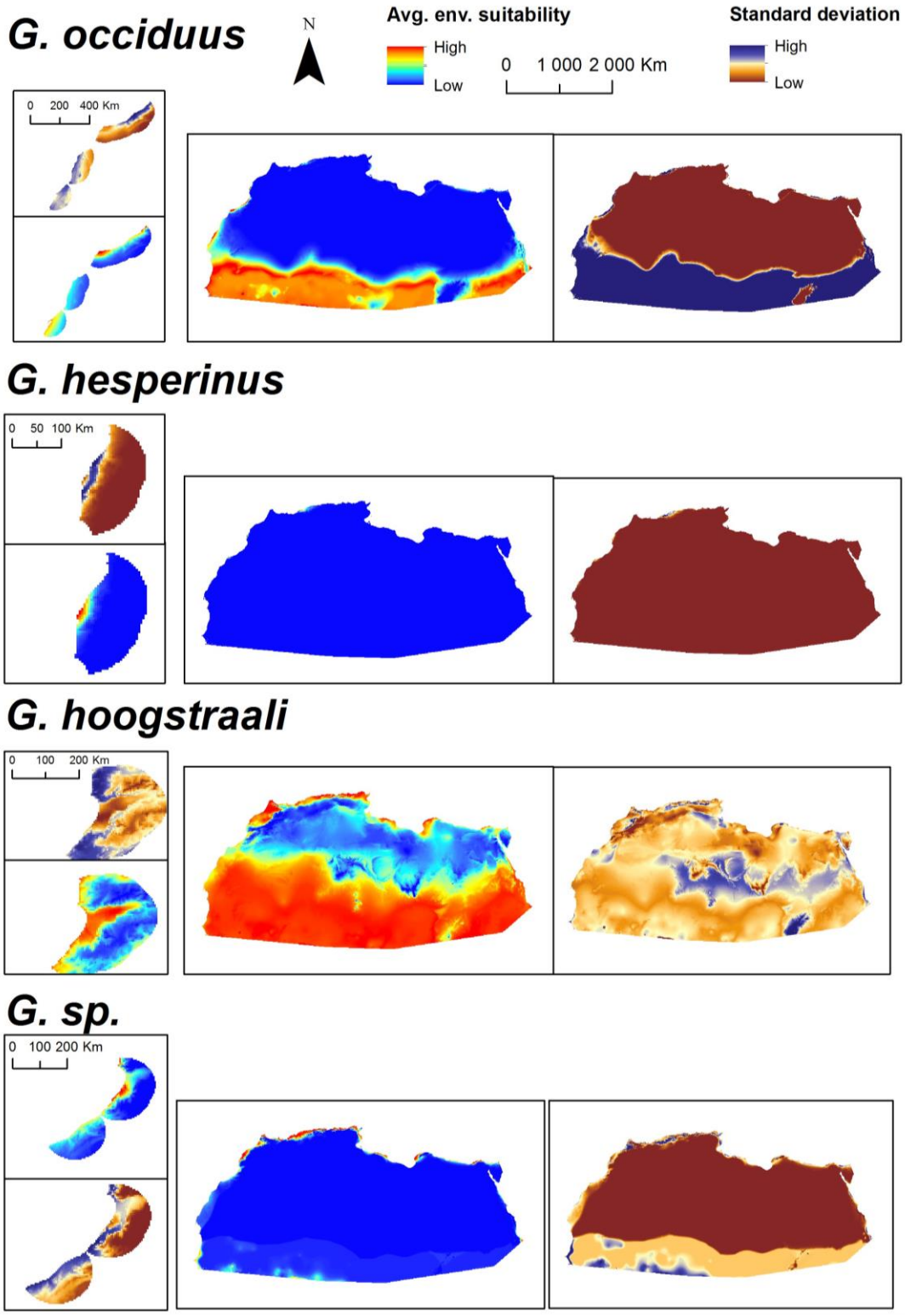

Fig. S25 Models of the coastal species using small training areas of 100 km around the species observations (left top) with corresponding standard deviations (Left bottom). Projections of the models to the current conditions of North Africa (Center) with corresponding standard deviations (right).

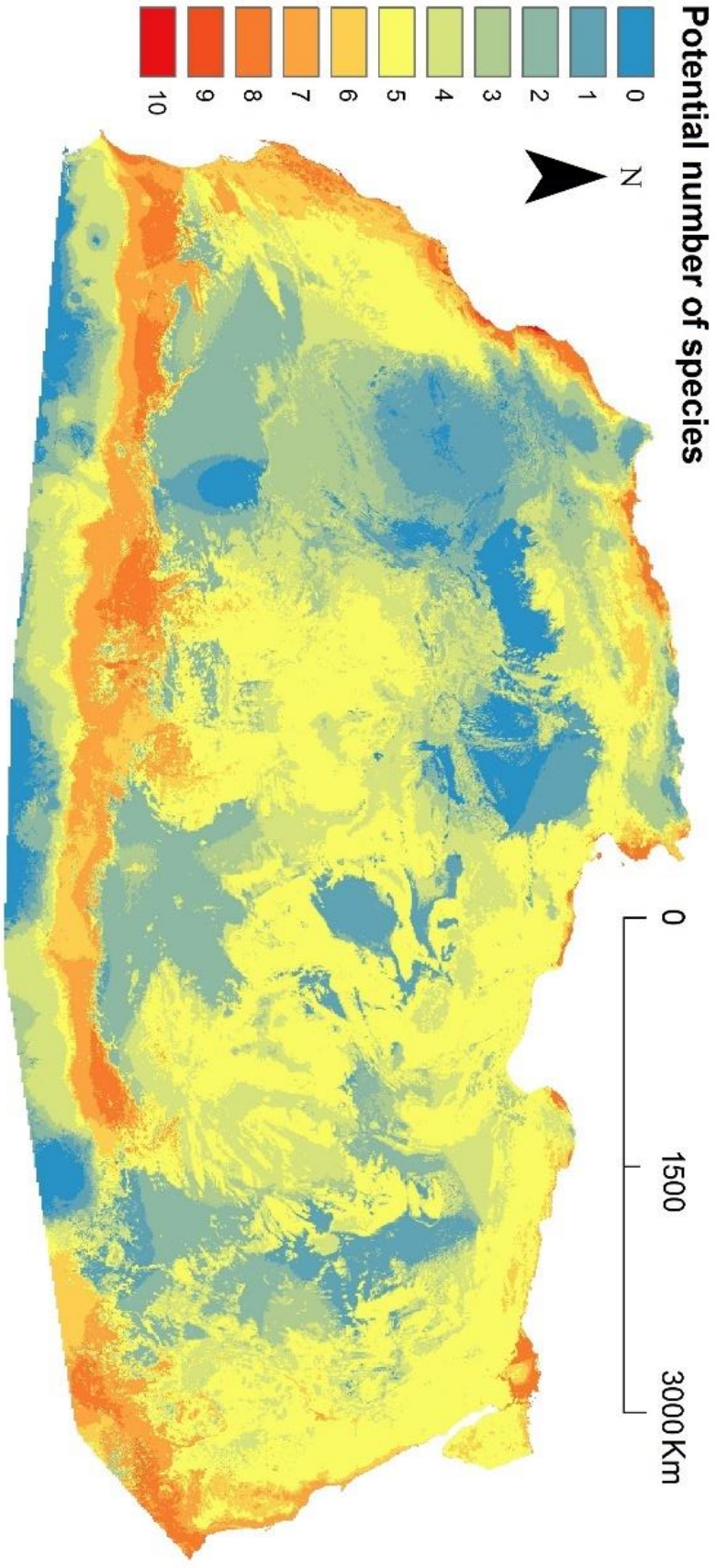

Fig. S26 Potential species richness, based on the ecological models of every considered species except for *Gerbillus sp.*. Warmer colors show areas with environmental suitability for most species at the same time (Maximum 11) and colder colors show areas with environmental suitability for the least species (Minimum 0).

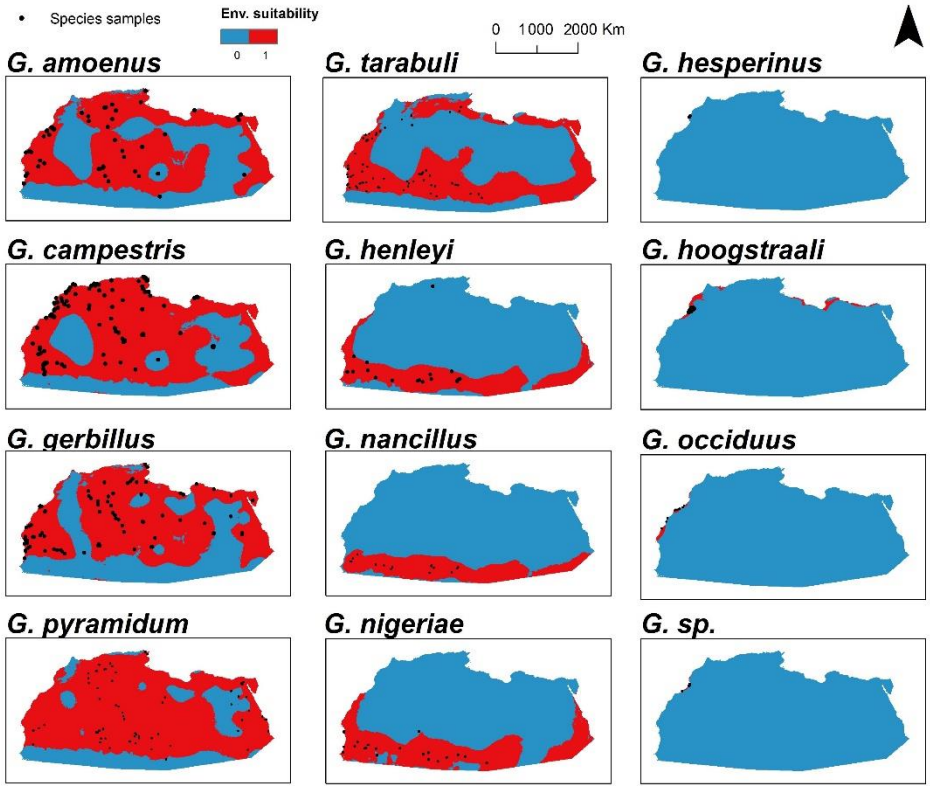

Fig. S27 Binary maps of climate suitability (1) or unsuitability (0), produced from the models of landcover and topo-climatic variables, applying a 5 per centile threshold.

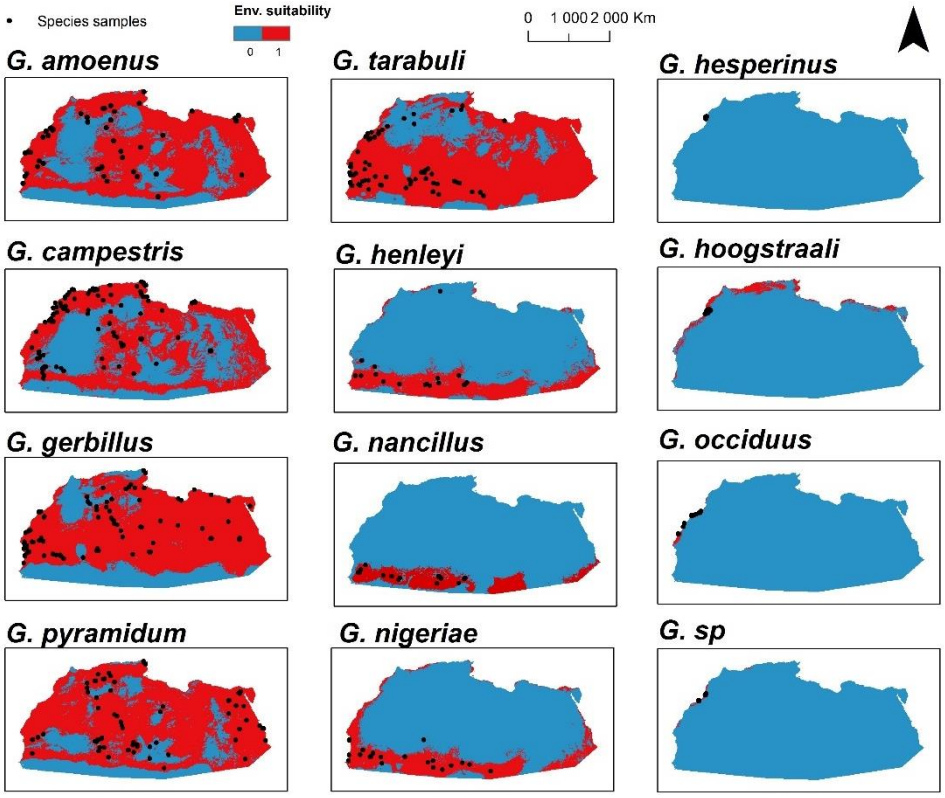

Fig. S28 Binary maps of environmental suitability (1) or unsuitability (0), produced from the models of landcover and topo-climatic variables, applying a 5 per centile threshold.

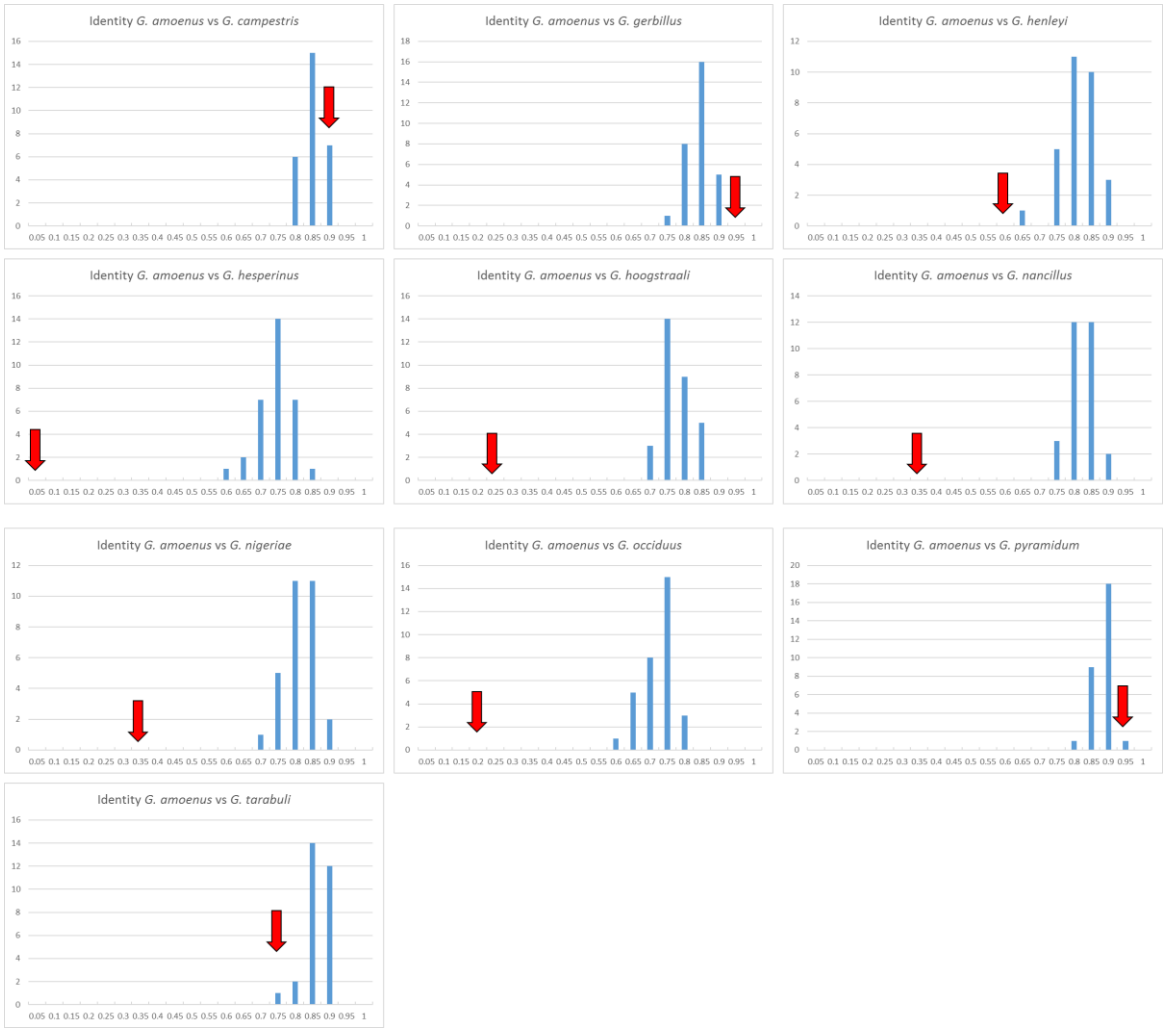

Fig. S29 Distributions of climatic identity test pseudoreplicates for 10 pairs of species. Red arrow represents the value of Schoenner's D.

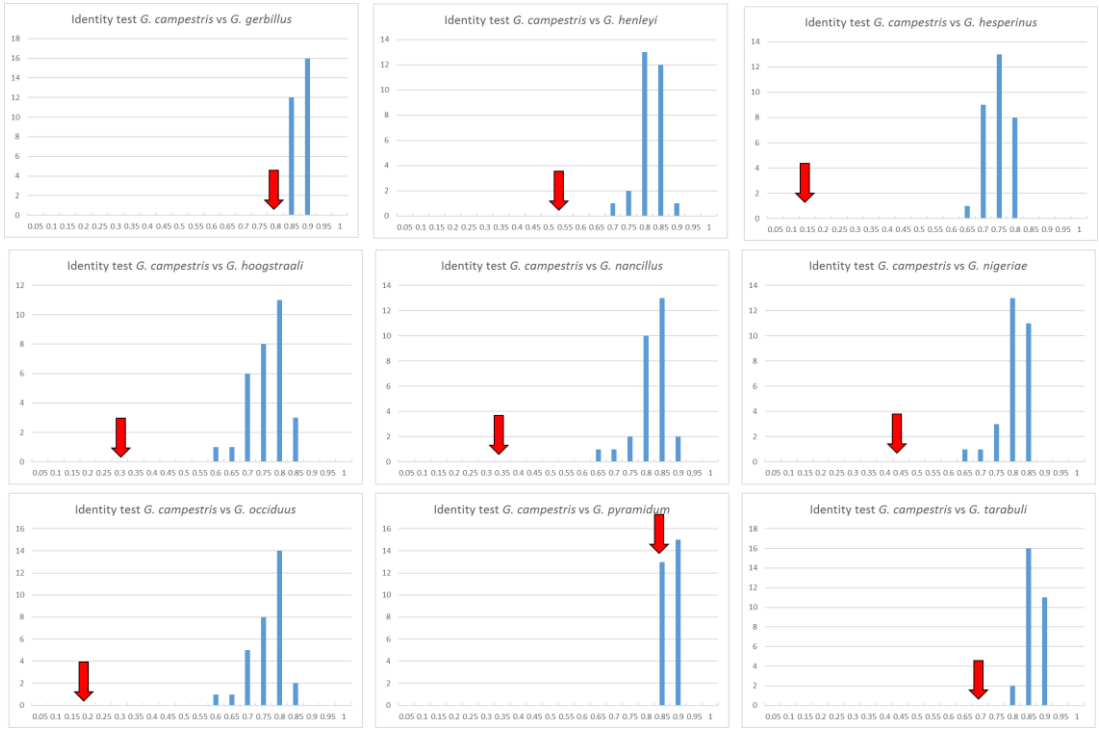

Fig. S30 Distributions of climatic identity test pseudoreplicates for 9 pairs of species. Red arrow represents the value of Schoenner's D.

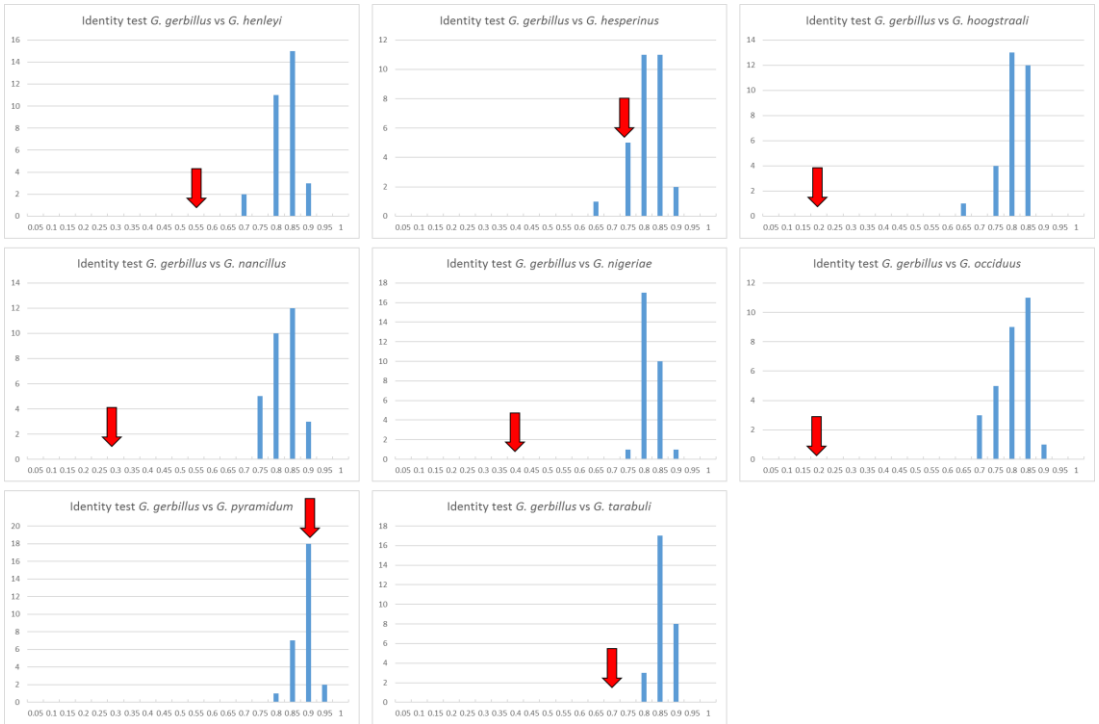

Fig. S31 Distributions of climatic identity test pseudoreplicates for 8 pairs of species. Red arrow represents the value of Schoenner's D.

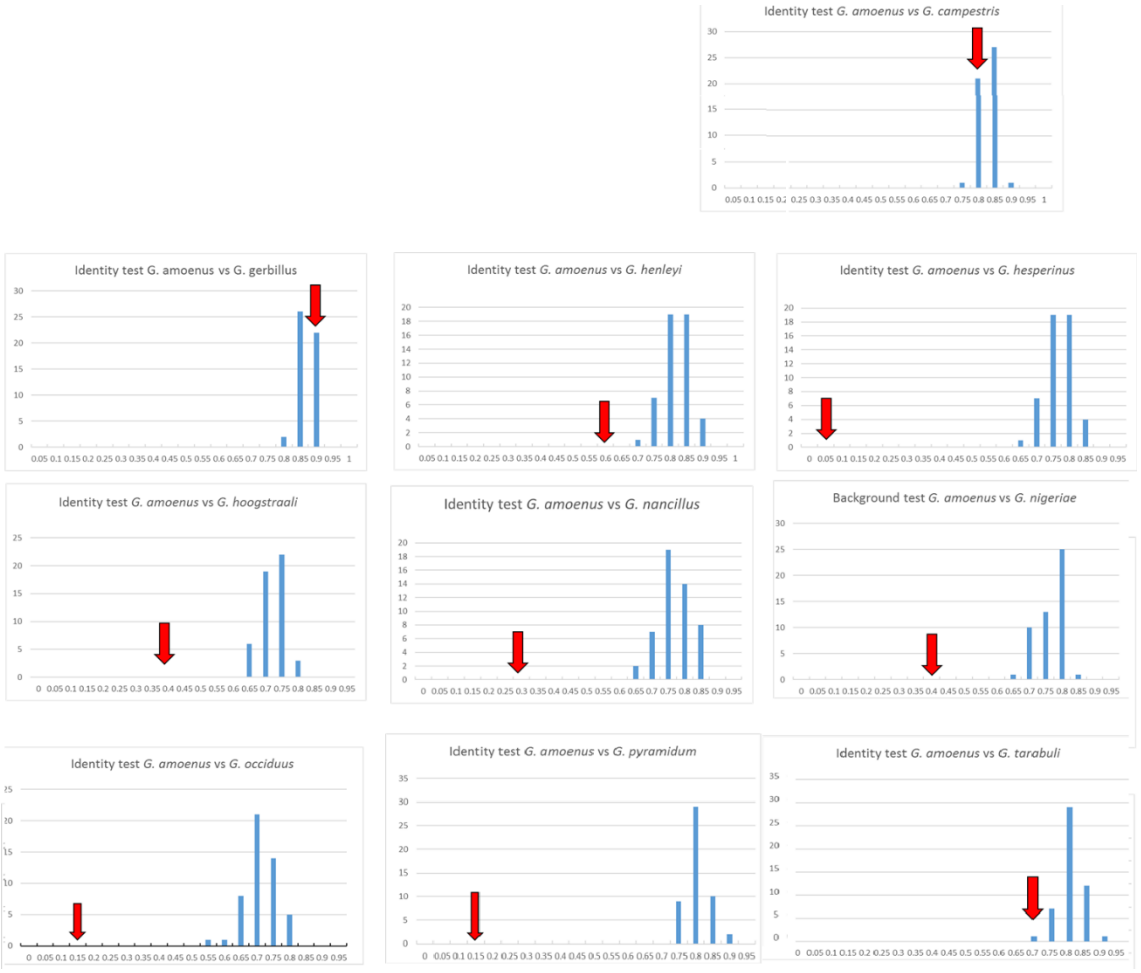

Fig. S32 Distributions of environmental identity test pseudoreplicates for 10 pairs of species. Red arrow represents the value of Schoenner's D.

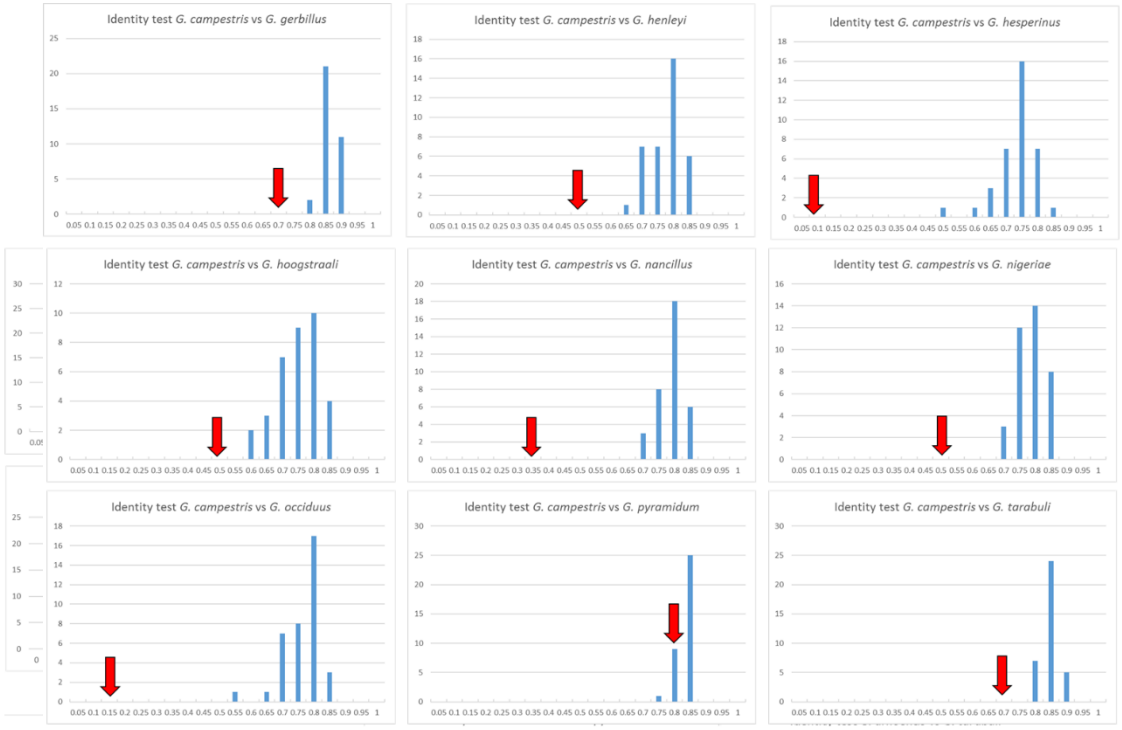

Fig. S33 Distributions of environmental identity tests for 9 pairs of species. Red arrow represents the value of Schoenner's D.

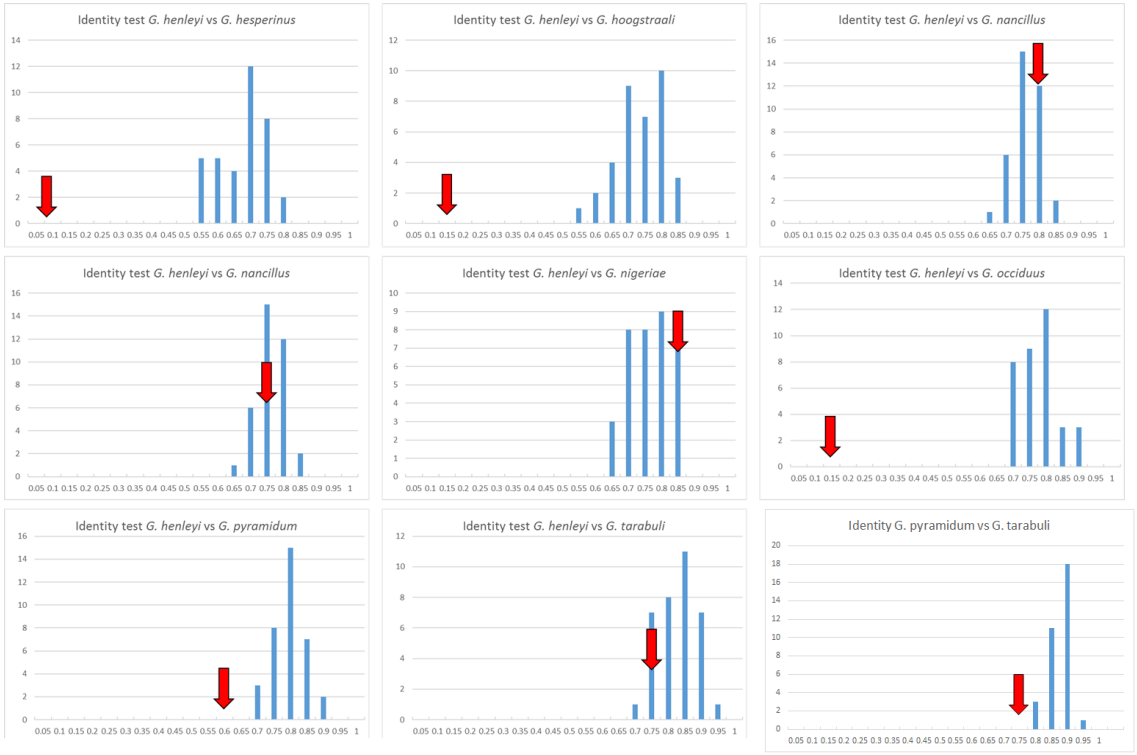

Fig. S34 Distributions of environmental identity tests for 9 pairs of species. Red arrow represents the value of Schoenner's D.

Fig. S35 Distributions of environmental identity tests for 11 pairs of species. Red arrow represents the value of Schoenner's D.

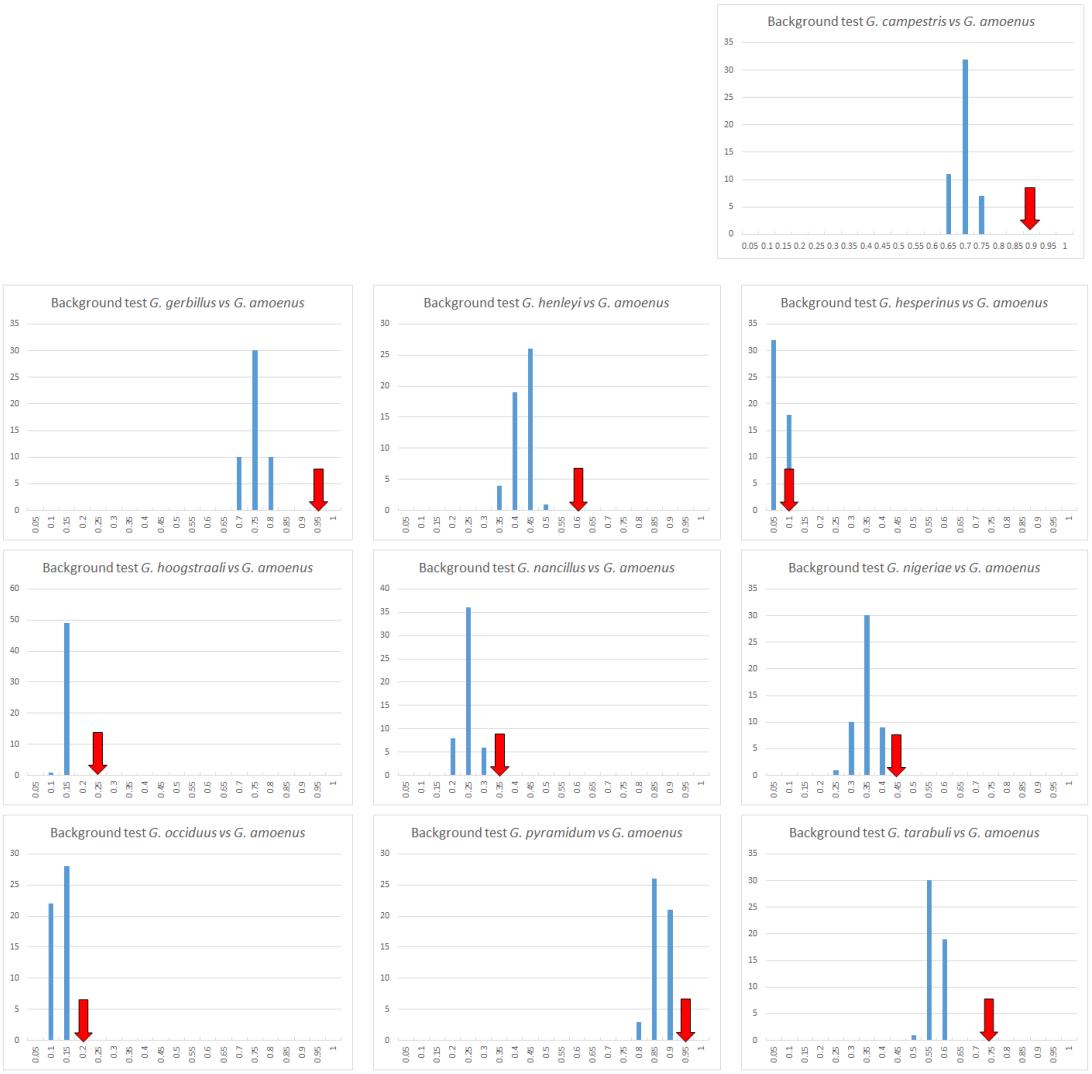

Fig. S36 Distributions of climatic background tests with *G. amoenus*. Red arrow represents the value of Schoenner's D.

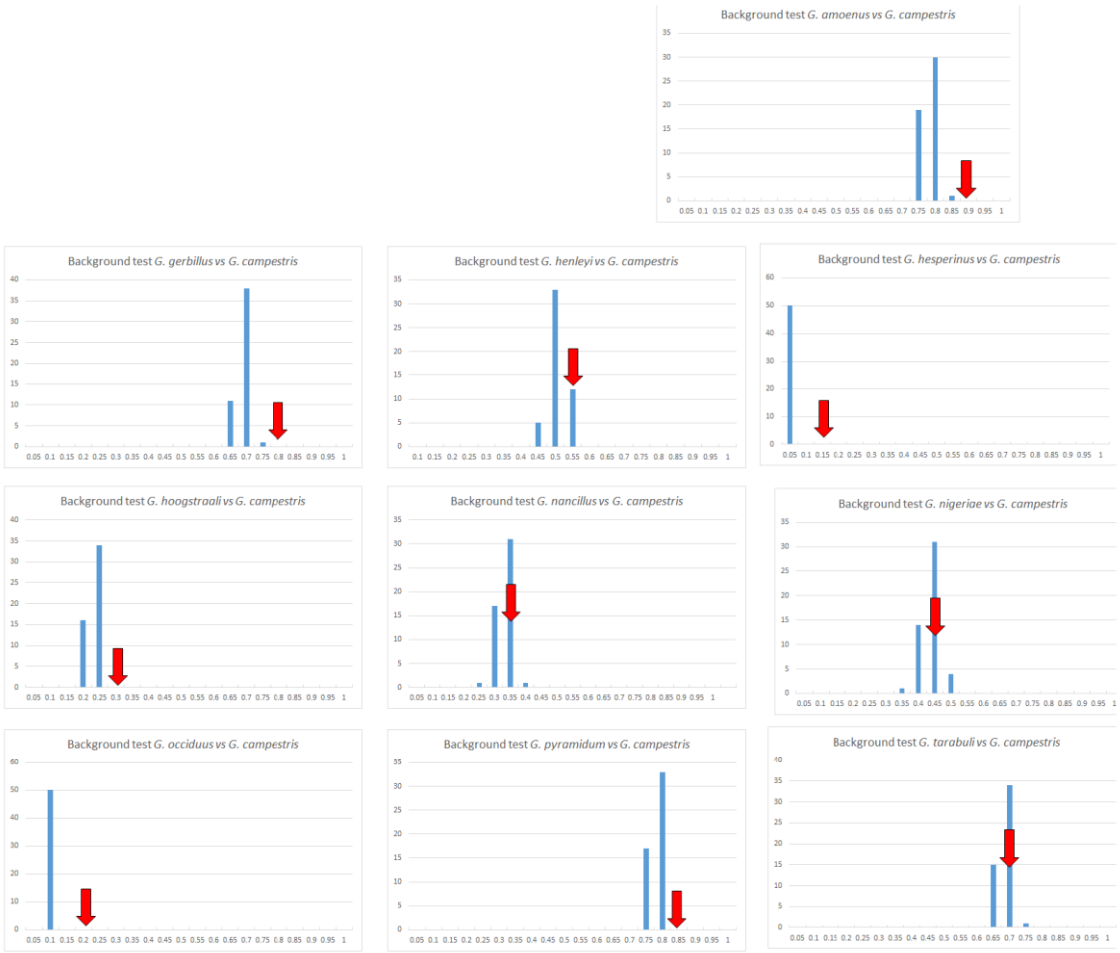

Fig. S37 Distributions of climatic background tests with *G. campestris*. Red arrow represents the value of Schoenner's D.

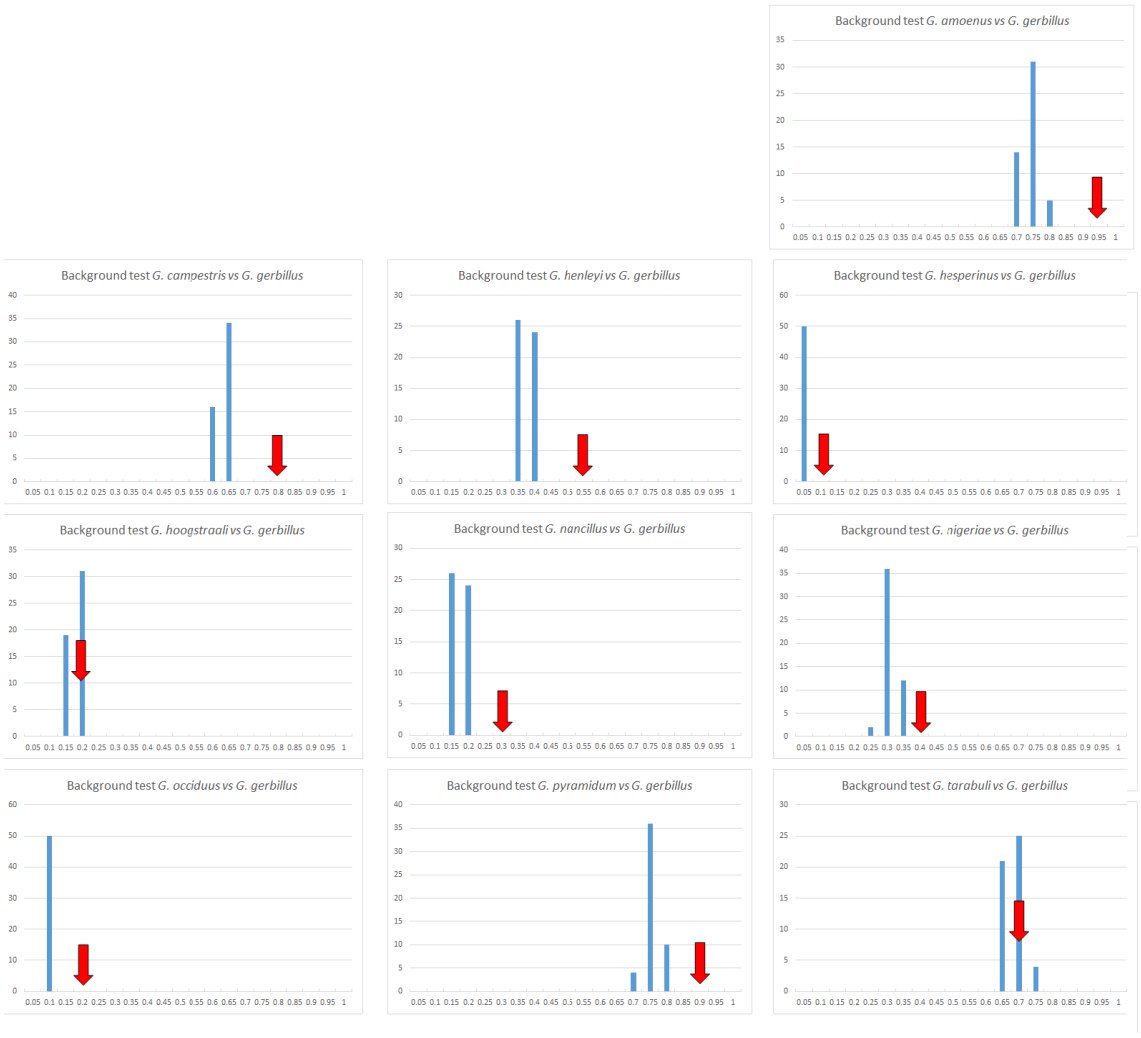

Fig. S38 Distributions of climatic background tests with *G. gerbillus*. Red arrow represents the value of Schoenner's D.

Fig. S39 Distributions of climatic background tests with *G. henleyi*. Red arrow represents the value of Schoenner's D.

Fig. S40 Distributions of climatic background tests with *G. hesperinus*. Red arrow represents the value of Schoenner's D.

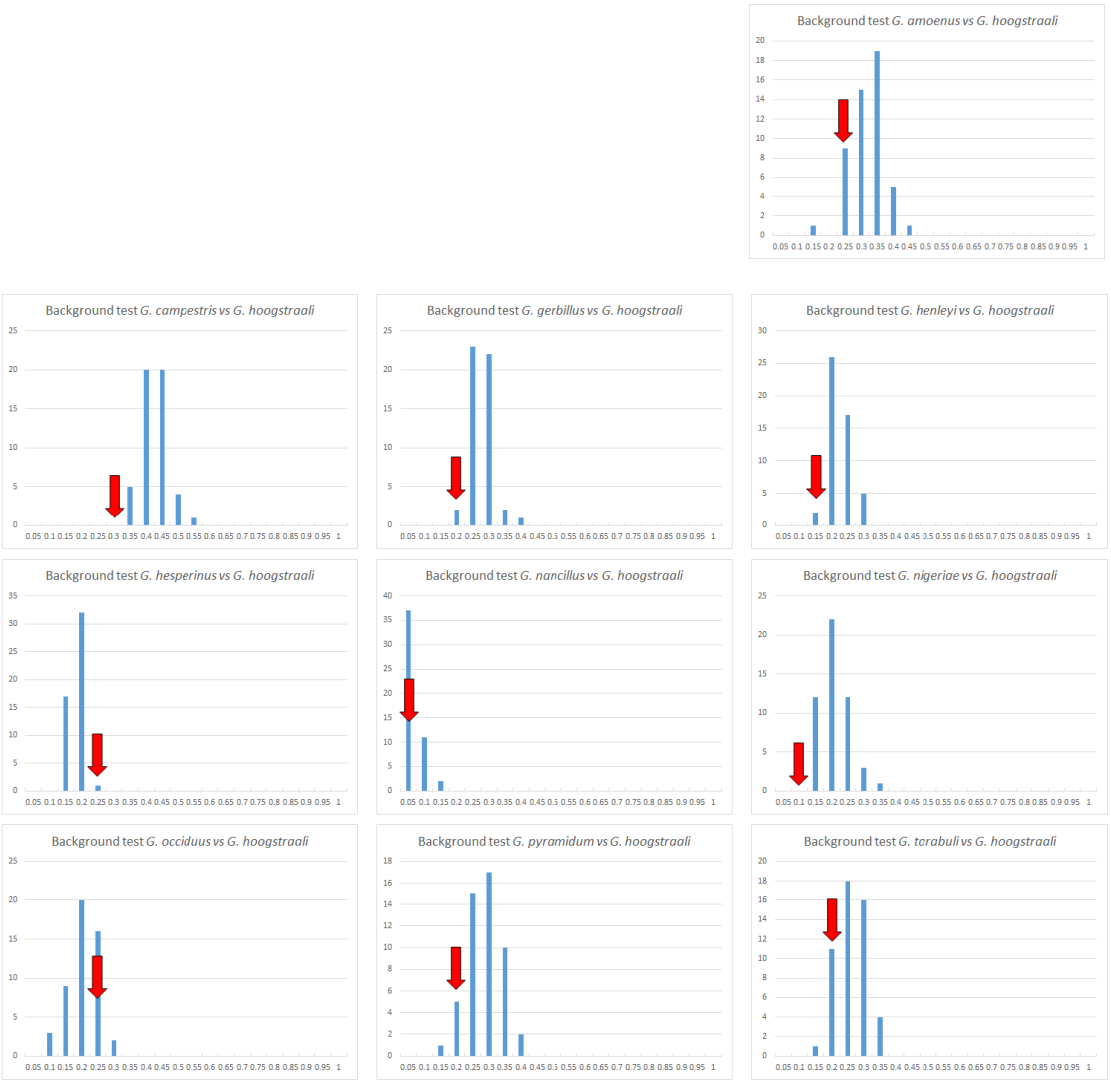

Fig. S41 Distributions of climatic background tests with *G. hoogstraali*. Red arrow represents the value of Schoenner's D.

Fig. S42 Distributions of climatic background tests with *G. nancillus*. Red arrow represents the value of Schoenner's D.

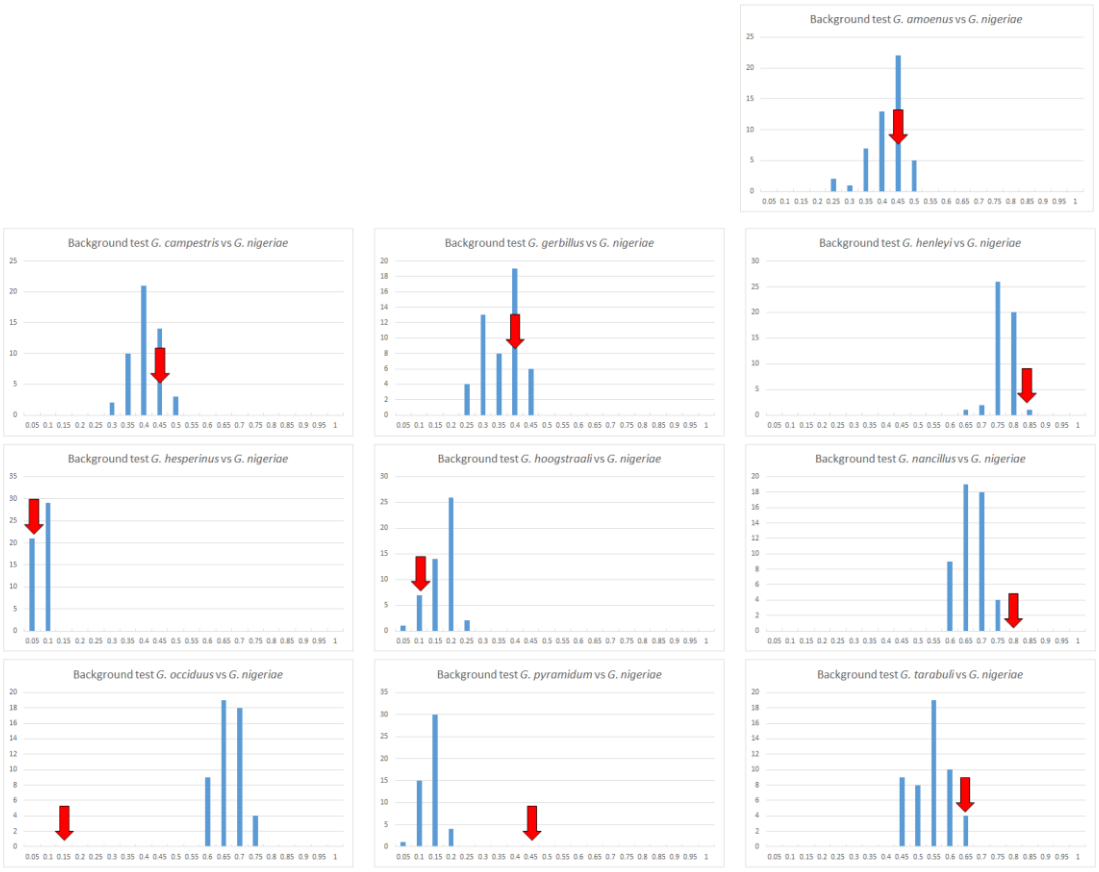

Fig. S43 Distributions of climatic background tests with *G. nigeriae*. Red arrow represents the value of Schoenner's D.

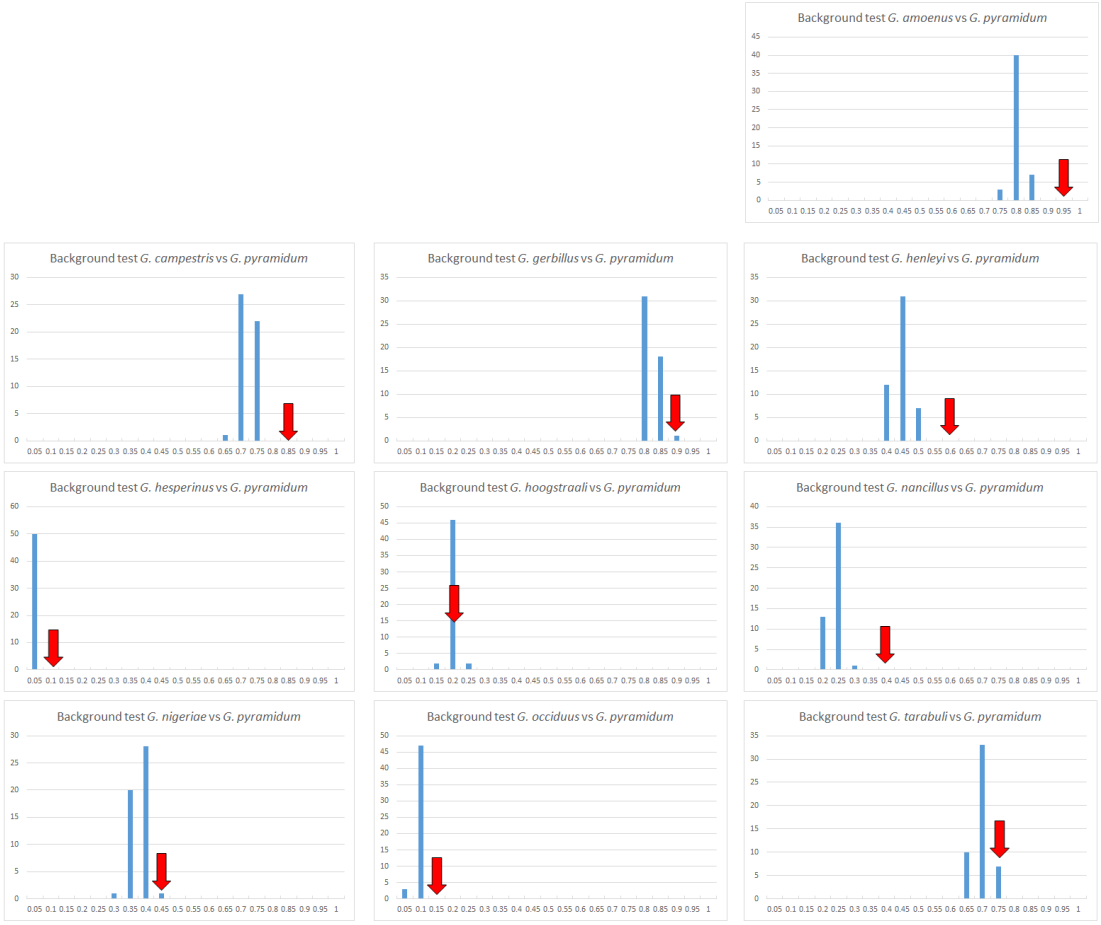

Fig. S44 Distributions of climatic background tests with *G. pyramidum*. Red arrow represents the value of Schoenner's D.

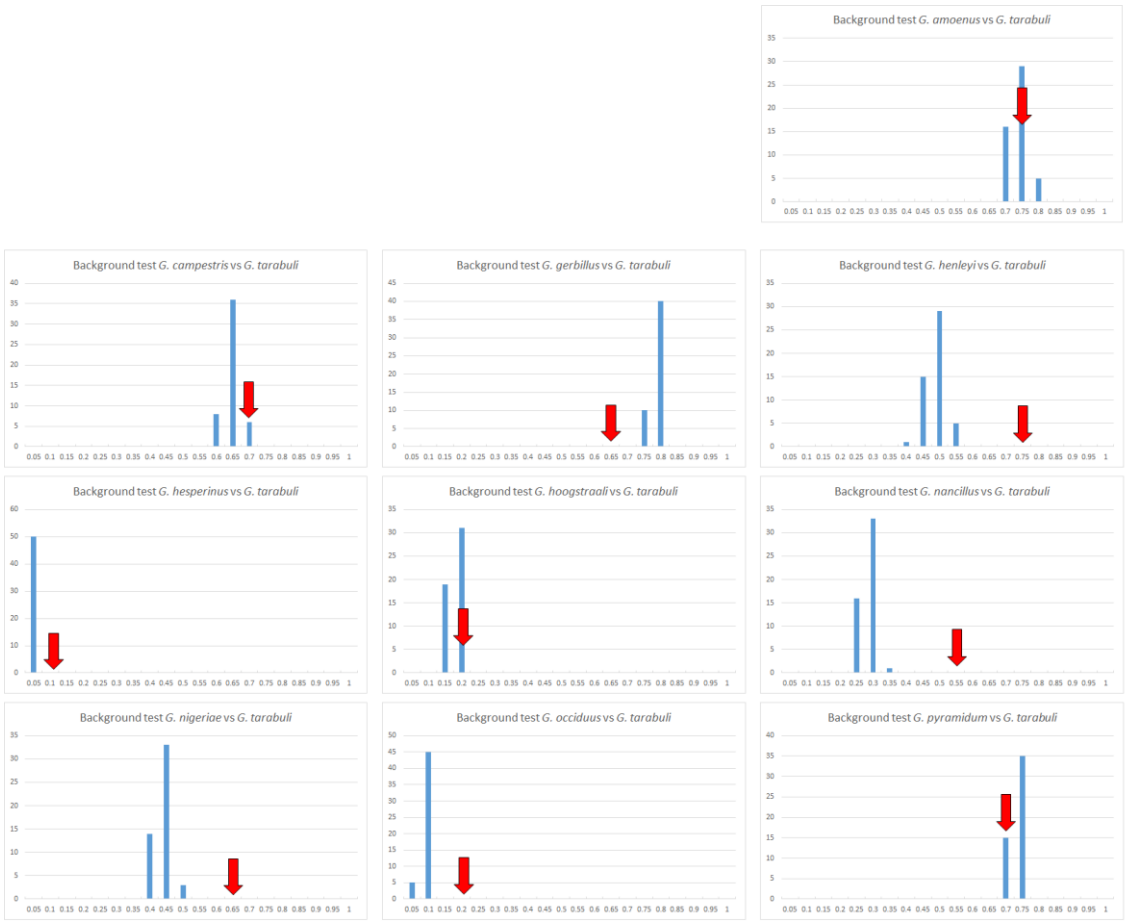

Fig. S45 Distributions of climatic background tests with *G. tarabuli*. Red arrow represents the value of Schoenner's D.

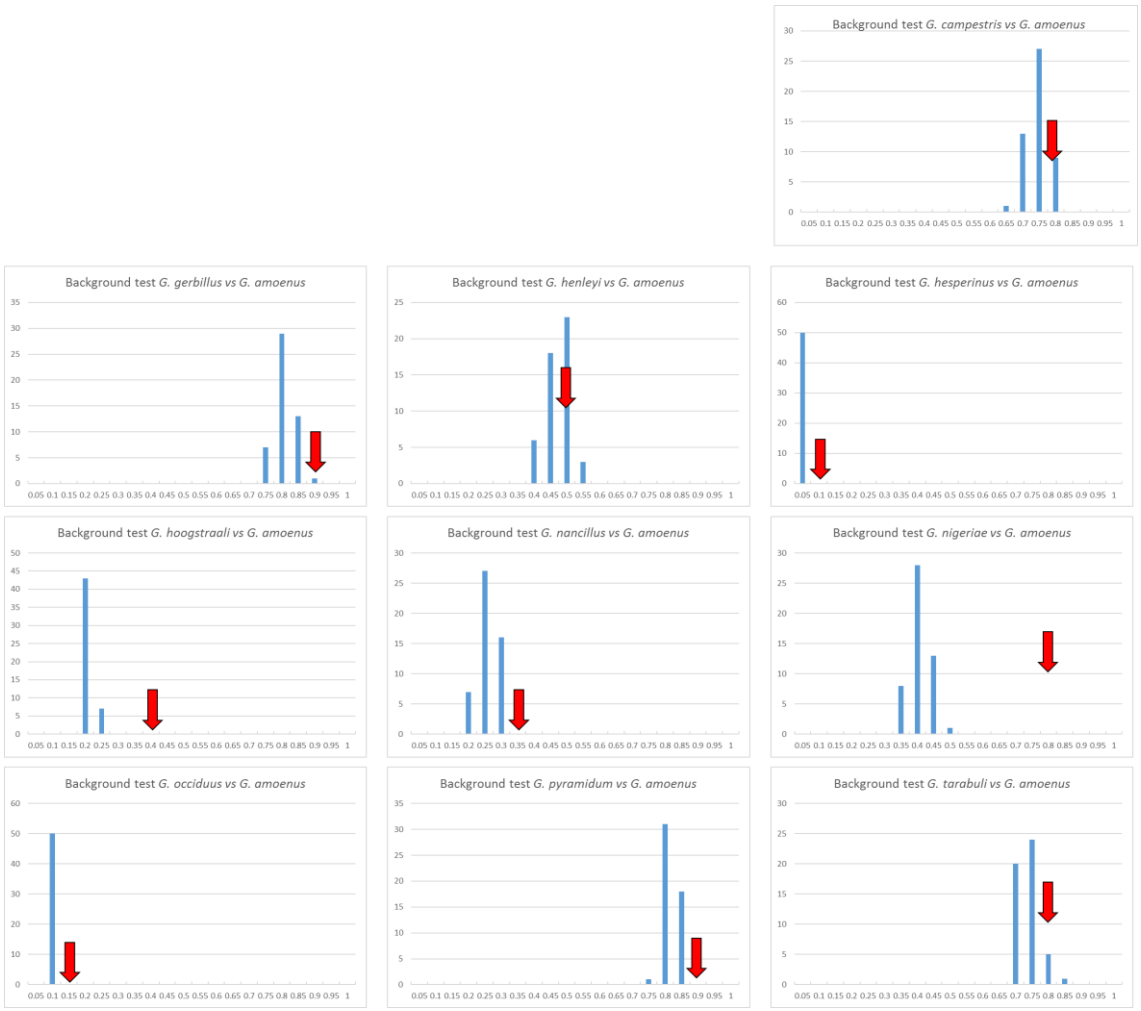

Fig. S46 Distributions of environmental background tests with *G. amoenus*. Red arrow represents the value of Schoenner's D.

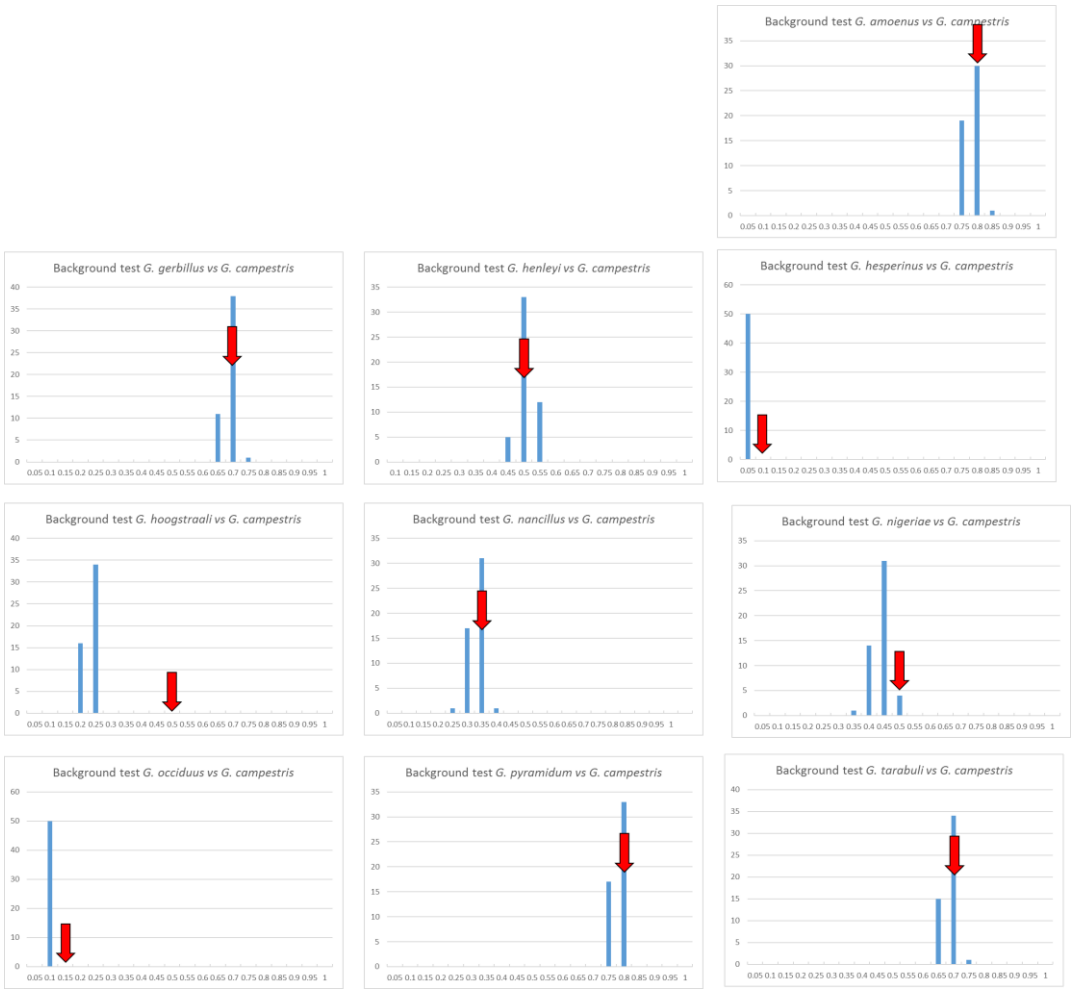

Fig. S47 Distributions of environmental background tests with *G. campestris*. Red arrow represents the value of Schoenner's D.

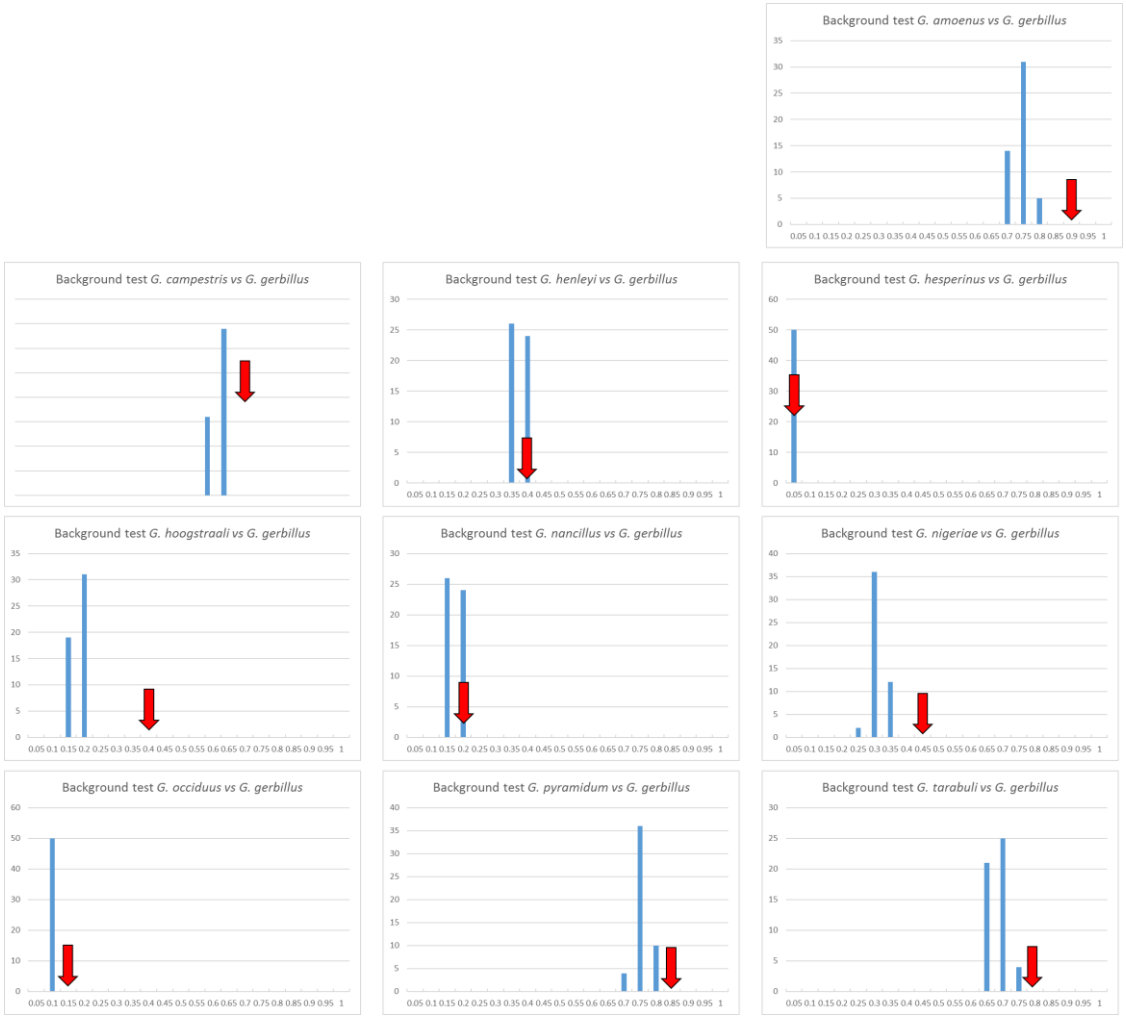

Fig. S48 Distributions of environmental background tests with *G. gerbillus*. Red arrow represents the value of Schoenner's D.

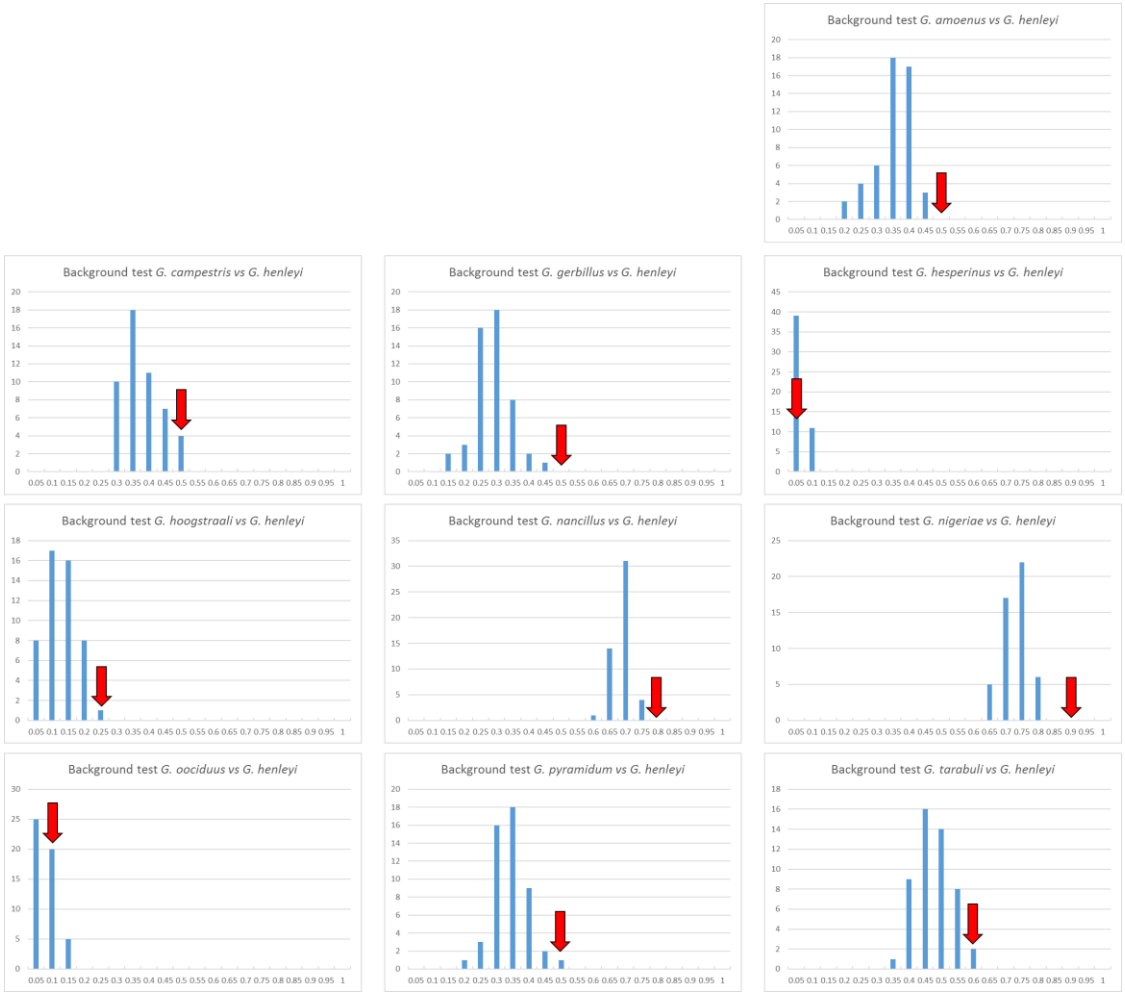

Fig. S49 Distributions of environmental background tests with *G. henleyi*. Red arrow represents the value of Schoenner's D.

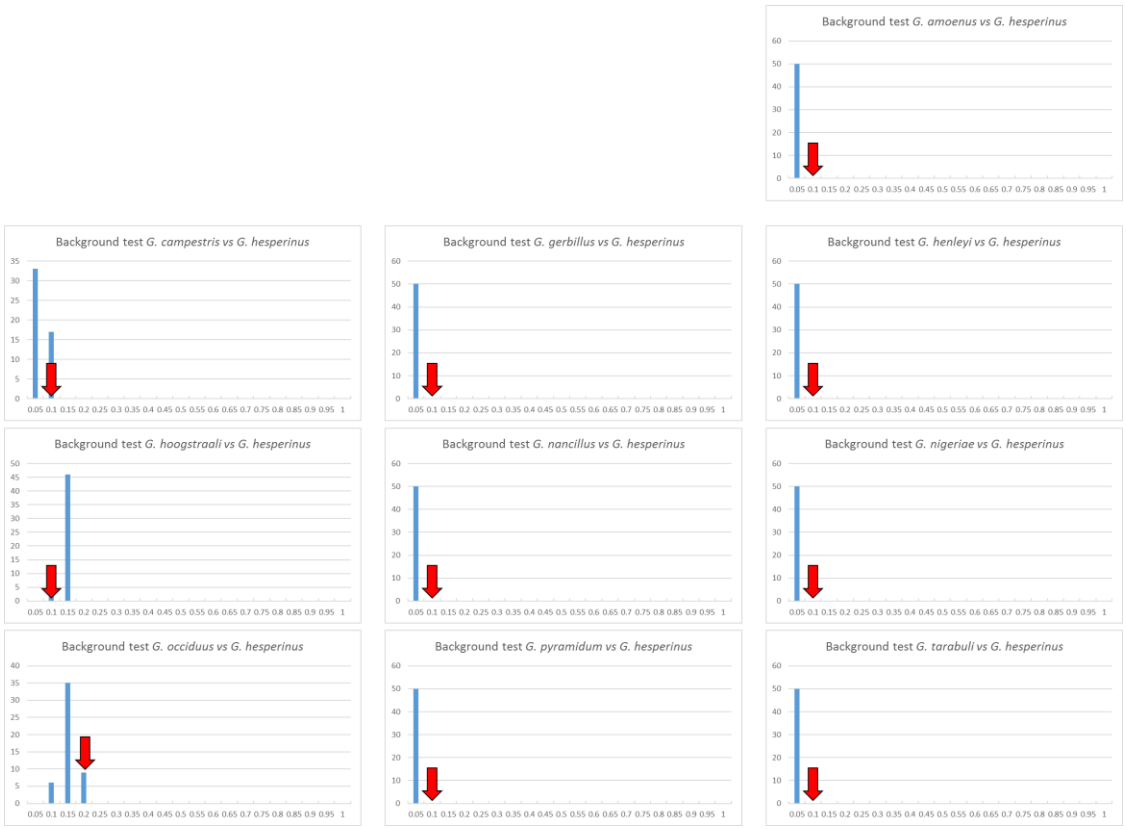

Fig. S50 Distributions of environmental background tests with *G. hesperinus*. Red arrow represents the value of Schoenner's D.

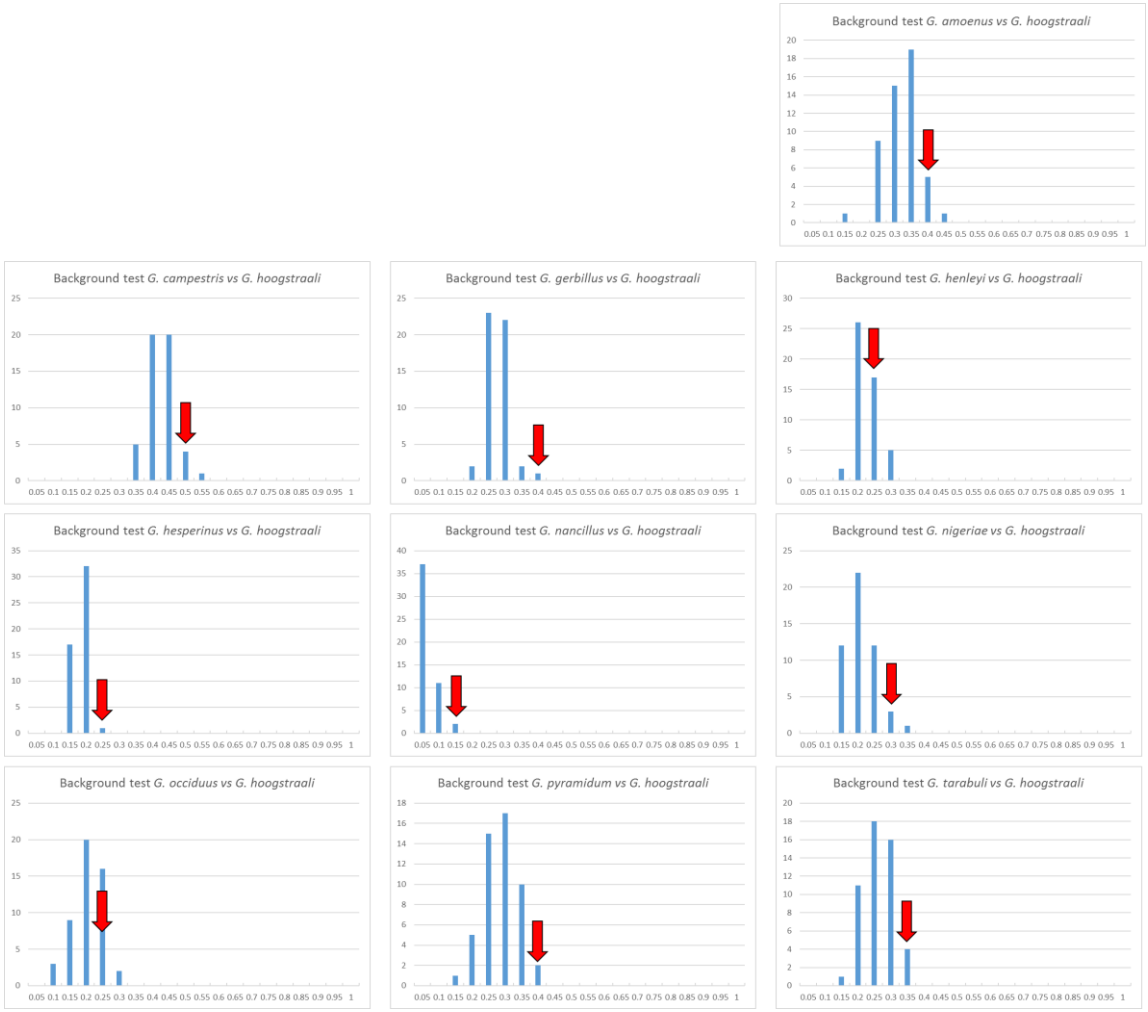

Fig. S51 Distributions of environmental background tests with *G. hoogstraali*. Red arrow represents the value of Schoenner's D.

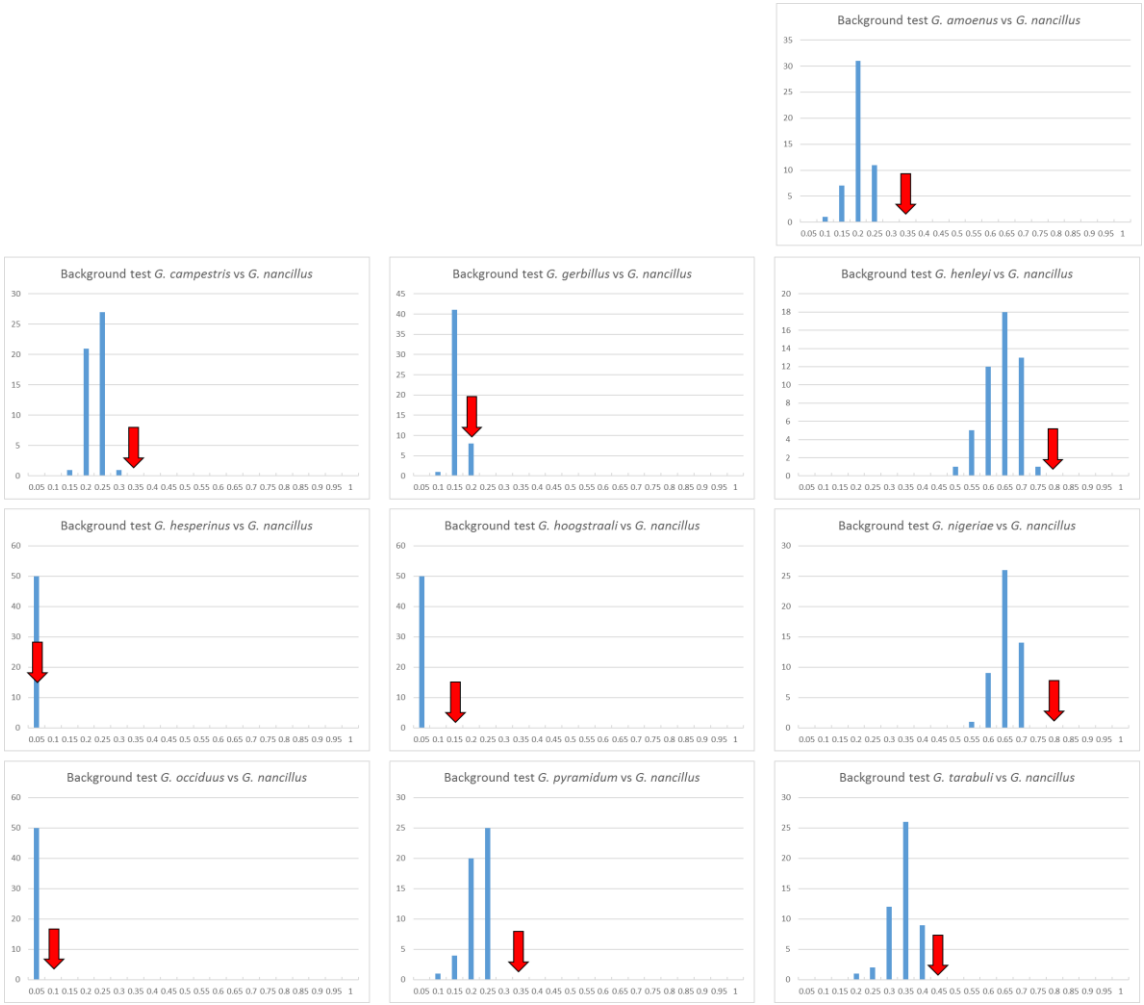

Fig. S52 Distributions of environmental background tests with *G. nancillus*. Red arrow represents the value of Schoenner's D.

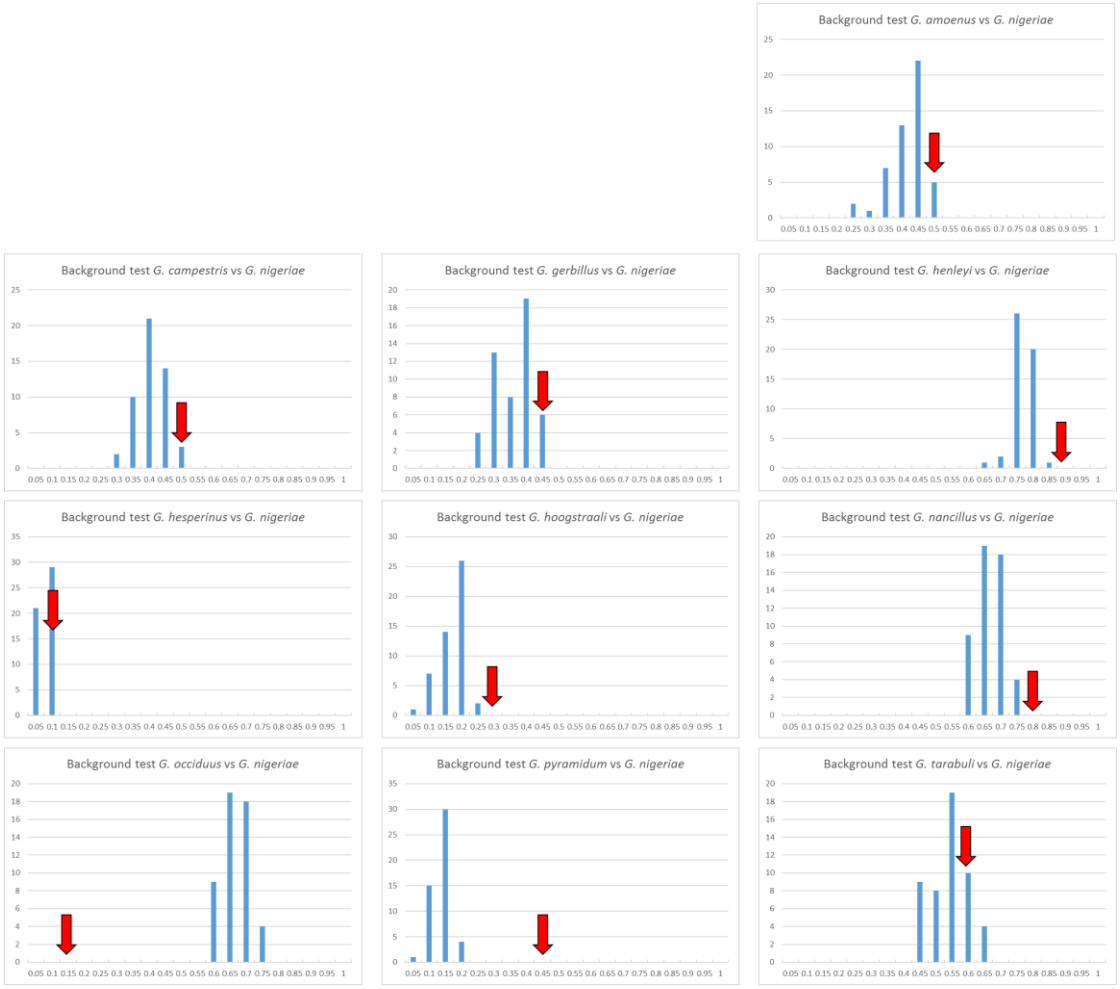

Fig. S53 Distributions of environmental background tests with *G. nigeriae*. Red arrow represents the value of Schoenner's D.

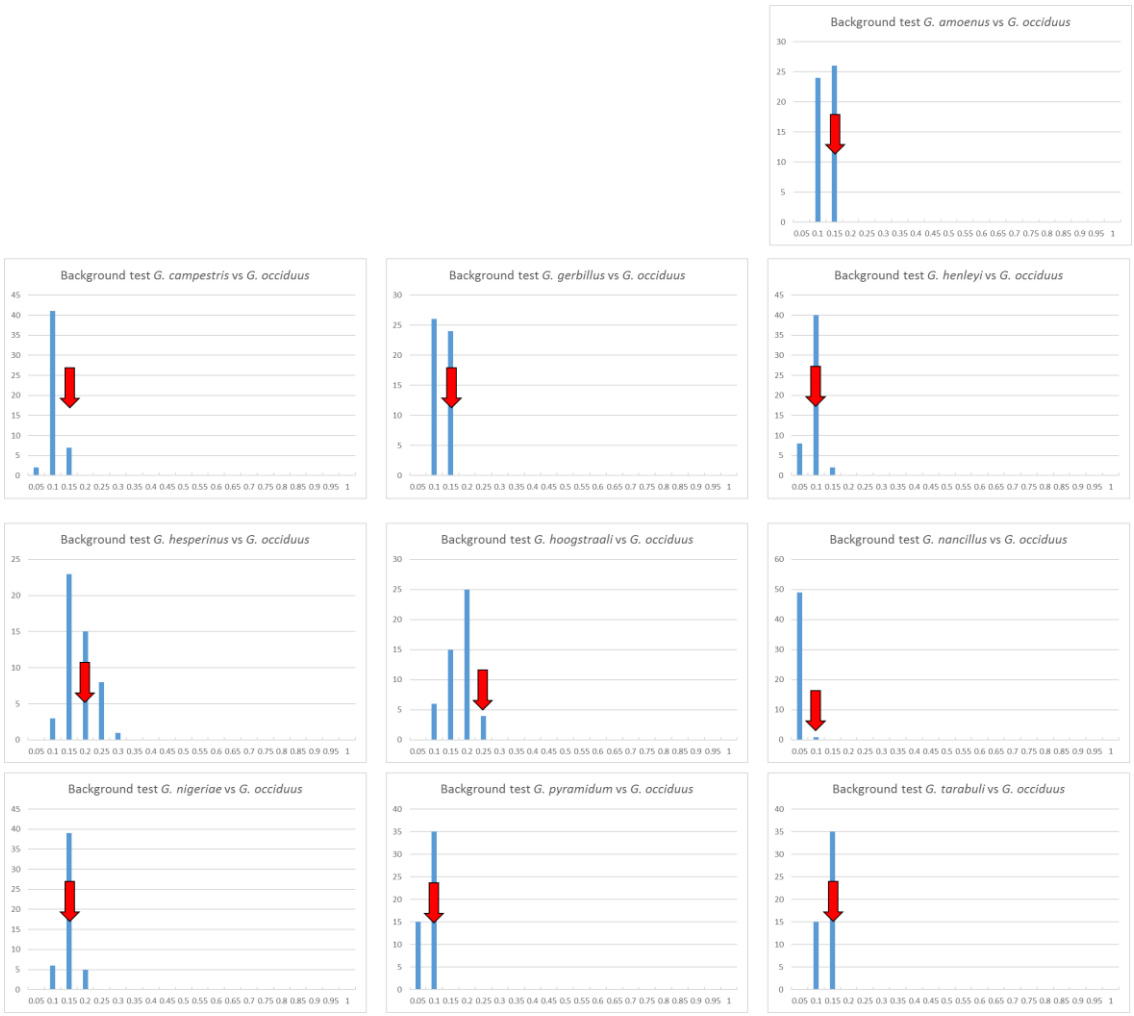

Fig. S54 Distributions of environmental background tests with *G. occiduus*. Red arrow represents the value of Schoenner's D.

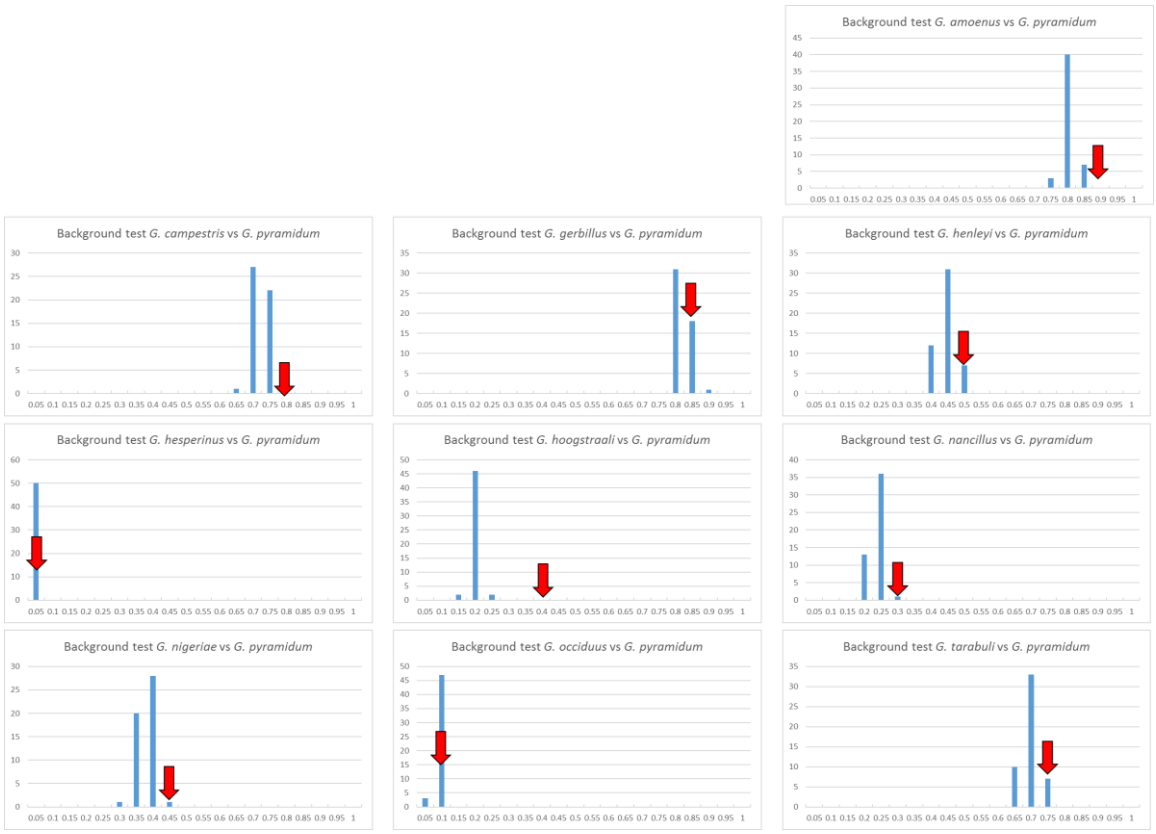

Fig. S55 Distributions of environmental background tests with *G. pyramidum*. Red arrow represents the value of Schoenner's D.

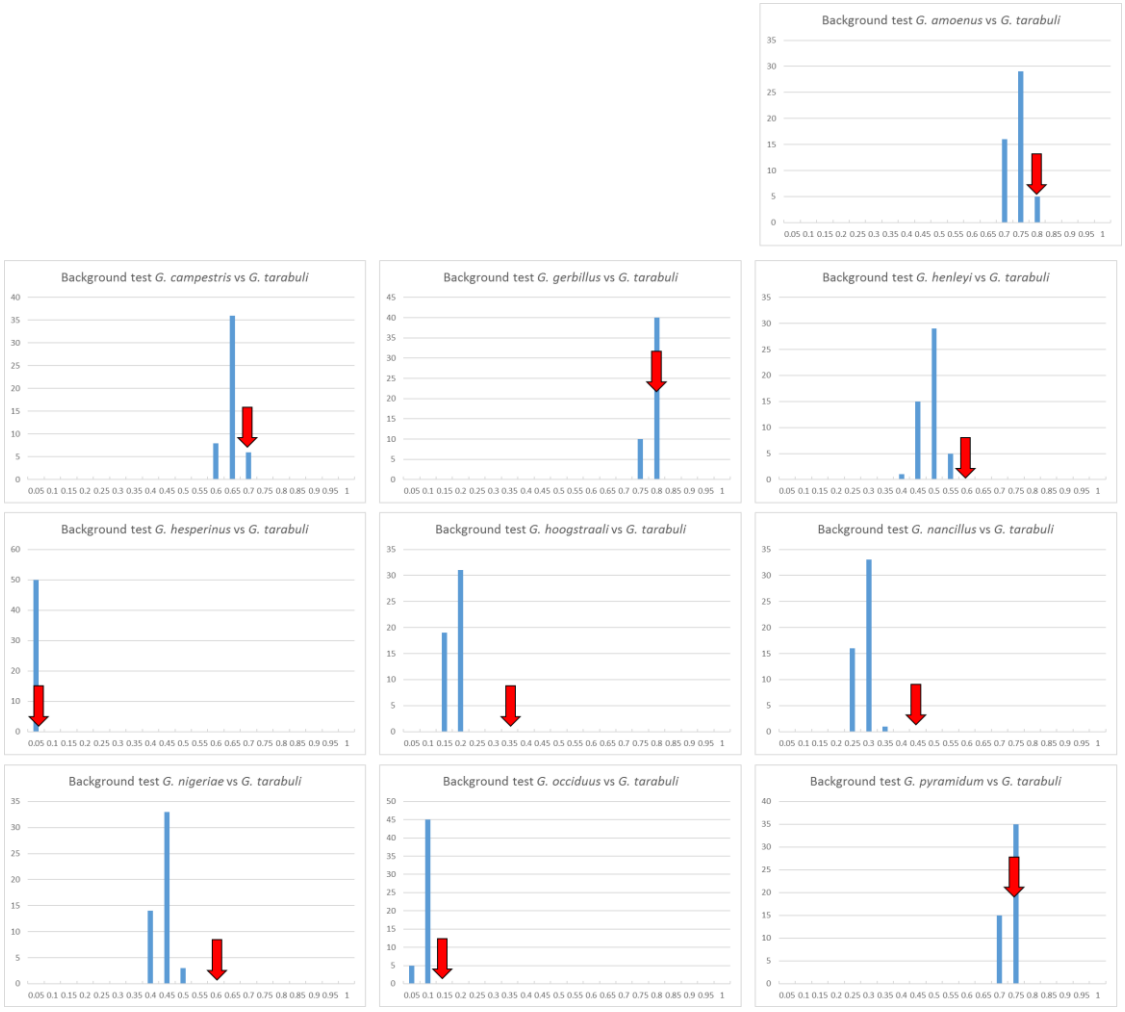

Fig. S56 Distributions of environmental background tests with *G. tarabuli*. Red arrow represents the value of Schoenner's D.